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OBITUARY NOTICES

MISS E. R. SAUNDERS, F.L.S.

1865–1945

Miss E. R. Saunders died in Cambridge on 6 June 1945, as the result of a cycling accident. She will be much missed by a large circle of botanists, for not only was she a familiar and much appreciated figure at meetings of the Linnean and Genetical Societies and of the British Association, but during her long teaching career she was in contact with many students who will remember vividly the vigour and lucidity of her expositions and her complete devotion to her work.

Miss Saunders was born in 1865 and was educated at Handsworth Ladies' College and at Newnham College, Cambridge. After obtaining First Class Honours in Part II of the Natural Sciences Tripos, she was awarded a research studentship by the College, and a year later was appointed demonstrator in Natural Sciences. Later she became Director of Studies in Natural Sciences at Newnham, a post which she held until 1925. Until students of the Women's Colleges at Cambridge were admitted to the University courses, Miss Saunders played a leading part in organizing the teaching of biological subjects for both Newnham and Girton. She cherished very happy memories of these strenuous early days, when much work had to be done with very inadequate facilities, but when, also, the thought that in learning to appreciate and add to scientific knowledge women were penetrating into a new world provided the stimulus which enabled her and her colleagues triumphantly to overcome all their difficulties.

Miss Saunders's mind had a fine incisive quality, and she brought both to teaching and research a full appreciation of scientific method and thought. By virtue of this she played a particularly distinguished part in the development of scientific botany during the first twenty-five years of this century, and the esteem in which she was held by her scientific colleagues is indicated by her election to the presidency of the Botanical Section of the British Association in 1920 and to the presidency of the Genetical Society in 1936. She was also awarded the Banksian Medal of the Royal Horticultural Society in 1906. Those who shared with her the tasks of laboratory demonstration will remember her remarkable skill in handling plant material and her unfailing alertness to challenge every casual interpretation. At the discussions of demonstrators following each laboratory class she would, almost invariably, lead the whole company (some rather flagging, perhaps) behind her in some minor research or investigation suggested by the class work.

The first research undertaken by Miss Saunders was a study of the structure and function of the septal glands of *Kniphofia*, but she soon became one of the enthusiastic band of workers who were engaged under William Bateson in investigating the phenomena of inheritance in plants and animals. She was concerned mainly with the genetics of the garden stock, *Matthiola incana*, and between 1900 and 1920 she published a number of papers on inheritance in this plant. During her investigations she became interested in some of the morphological peculiarities shown by the plants with which she was working, notably the lines of hairs on the stems of some specimens of *Matthiola* and

the abnormalities of the gynoecium in others. Neither of these phenomena could be explained satisfactorily according to current morphological ideas, and Miss Saunders set herself the task of attempting to elucidate them. From her observations on the lines of hairs on the stems arose her 'leaf-skin' theory of the structure of the stem of flowering plants, and from her observations on the abnormalities of the gynoecium arose her theory of carpel polymorphism. This theory is based on extremely detailed observations on the structure of the gynoecium in many families of flowering plants, which are in themselves an important addition to our knowledge of the morphology of the angiosperms. Substantial series of her scientific papers in this field appeared especially in the *Annals of Botany*, the publications of the Linnean Society, and the *New Phytologist*; the culmination of her work on the structure of the gynoecium was the publication in 1938 and 1939 of the two volumes of her book *Floral Morphology*, in which her results were summarized and integrated.

Miss Saunders's views on floral morphology are best appreciated by reading certain of her more recent papers in which she was defending her position against critics. Best of all, perhaps, are the vigorous comments on 'Floral Anatomy and its Morphological Interpretation' (*New Phytol.* 33 (1934), 127–69). Here the case for a close study of the anatomy of a flower as a clue to its recent phylogenetic history is argued vehemently and unanswerably from a great body of facts derived from her own investigations. In particular, she makes the point that vascular bundles may persist after the floral members which they supplied in ancestral types have been lost in the morphological sense. Species of the Primulales supply a series showing progressive loss of the antesepalous stamens, but with the retention, in the corolla, of their vascular supply. Another magnificently written paper, 'The Vascular Ground-Plan as a Guide to the Floral Ground-Plan: Illustrated from the Cistaceae' (*New Phytol.* 35 (1936), 47–67), carries the argument an important step further, and relates the unusual position and asymmetric form of the petals in Cistaceae to a torsion suffered by their vascular bundles. The well-known Theory of Carpel Polymorphism is based on precisely these kinds of arguments, and it stands or falls, as a useful morphological concept, on the validity of generalizing the two theses of the profound conservatism of the vascular ground-plan and, to a lesser degree, of the determination of form by structure. For all the skill in marshalling her great army of facts and for all the controversial vigour of her style, we cannot help but consider that Miss Saunders put too much faith in her premises. Her outlook was too much phylogenetic and too little morphogenetic. She was reluctant to concede a reciprocal determination of structure by form and function or to allow that the vascular system may show plasticity and opportunism as well as conservatism. But it must be acknowledged that the 'stubborn and irreducible facts' of floral structure, especially of the Cruciferae, to which she drew attention, are still not satisfactorily explained by any rival theory; and her name will certainly always be remembered when these topics are discussed.

At the outbreak of the war, with characteristic decisiveness and courage she abandoned her research work and sought a full-time war post, which she filled until 1945. The war completed, she felt that she still had many problems left to solve, and she was returning with undiminished enthusiasm to her scientific work when she met with the accident which caused her death. This return to active scientific work at the age of nearly 80 indicates very clearly the salient features of Miss Saunders's character: her devotion to science, her vigour, and the thoroughness and consistency of her mind which made it

Lafayette

PROFESSOR J. H. PRIESTLEY, D.S.O., B.Sc., F.L.S.

1883–1944

intolerable to her to feel that she had not fulfilled her intentions down to the last detail. Those who knew her will also remember her kindness and her delightful, quiet humour, and will feel that by her death the botanical world has lost a notable figure who was regarded with great respect and affection.

A. R. CLAPHAM, M. R. GILSON AND H. GODWIN

JOSEPH HUBERT PRIESTLEY, D.S.O., B.Sc., F.L.S.
1883–1944

Joseph Hubert Priestley was born at Tewkesbury and educated at Tewkesbury Grammar School (of which his father was Headmaster) and at University College, Bristol, from which he took his London Degree. At Bristol, though primarily a student of Botany, he also attended the Honours Courses in Chemistry and Physics, a training which gave him an exceptionally sound basis for his later physiological plant studies. He took charge of the Botany Department at Bristol in 1905 at the early age of 22 and was appointed to the Chair of Botany at Leeds University in 1911, in succession to Prof. V. H. Blackman. In 1914 he was in command of the University Officers' Training Corps and was one of the first to cross to France with the B.E.F.; from 1915 to 1919 he served on the Staff (Intelligence) being twice mentioned in dispatches and awarded the D.S.O. In 1919 he had the honour to become a Chevalier of the Crown of Belgium.

On his return to Leeds in 1919 he resumed his botanical work with the utmost vigour and at the same time his great interest and exceptional ability as an administrator became evident. From 1924 he served on the Finance Committee of the University, he had an exceptionally long term of office as Pro-Vice-Chancellor, part of which fell during a period of absence of the Vice-Chancellor, and he was also a most able Chairman of the Scholarships Committee; in fact he had so complete a grasp of all the complex details of University administration and the interrelationships of the Faculties that problems of almost every kind were constantly referred to him. He served for many years as a member, and finally as Chairman, of the Joint Matriculation Board.

As a teacher Priestley was quite outstanding; he never allowed his lectures or demonstrations to become stereotyped and would go to endless trouble to present matter in a novel and interesting way, so that his staff and students alike caught the infection of his own enthusiasm. His great interest in teaching brought him also in contact with teachers in local schools and Yorkshire Training Colleges, and meetings were arranged in the Department for discussions and demonstrations of new material likely to help them in their work. His great success as a teacher was linked with vigorous research, a memory for recorded detail, a realization of the significance of his facts and their possible practical bearing and above all a complete understanding of his fellow-men. His example as a teacher must be one of the most valued memories of his staff and the many students who have gone into the educational world.

His botanical work started in Bristol with F. L. Usher on the first products of photosynthesis; this was followed by a study of the effects of electricity on plant growth, but later his main interest became focused on developmental studies of plant tissues. These

studies were mainly published in the *New Phytologist* and the viewpoint was introduced by a series of physiological studies in plant anatomy in vols. 21 and 22. The object of these studies was to counterbalance the teleological viewpoint of Haberlandt and may be summed up in his own introductory words: 'It is true that, theoretically, Natural Selection may explain the existence of any useful working mechanism, but the mere demonstration of usefulness tends to draw a veil over the way in which the mechanism comes into being, and any real explanation of the structure must wait until its development has been traced and interpreted in terms of physico-chemical causation.' The inspiration for this line of research he took in the first place from the writings of Prof. W. H. Lang, and in the early phases of his work he frequently discussed conclusions with him. The first set of physiological studies was followed in 1925–6 by a series of *New Phytologist* papers on Light and Growth and in 1930 on the Physiology of Cambial Activity. During this period very considerable light was thrown on the endodermis and its rôle in water absorption, shoot and root growing apices and the differences in their development, cork formation and vegetative propagation. On this line of work a vigorous school of Botany grew up in Leeds, and as it was unique of its kind in this country contacts were made particularly with botanists in Europe and in the United States; many post-graduate students from overseas came to work in the Leeds laboratories and their subsequent publications bear witness to the inspiration they received from Priestley. His investigations of plant meristems later became particularly focused on the cambium and its derivative tissues and the many problems of tree growth which were brought to his notice as a member of the Forestry Commission. As President of Section K (Botany) at the British Association Meeting in York in 1932 he spoke on the subject of tree growth and new methods of studying cambial activity. His last paper on spiral grain in timber appeared in the *American Journal of Botany* after his death.

It is not possible in a short note to give any true impression of Priestley, either as a botanist or as a man, as it is seldom that one finds combined in one personality such ability as a teacher, investigator and administrator and such a human understanding. The respect and affection with which he was regarded is perhaps best illustrated in the relationships of Old Students to the Department. All who came in contact with him were invigorated by his refreshing personality and any problem, botanical, administrative or personal, received his careful consideration and was helped towards a solution by his wide experience, carefully balanced judgement and his own outstanding courage. Though he was not permitted to fulfil the normal period of University service, he maintained his interest in botanical matters to the end and left behind him a record of work and human endeavour which could be surpassed by few.

L. I. SCOTT

WATER RELATIONS OF PLANT CELLS

IV. DIFFUSION EFFECTS OBSERVED IN PLASMOLYSED TISSUES

By T. A. BENNET-CLARK and D. BEXON
King's College, London, and University College, Nottingham

(With 8 figures in the text)

Introduction

Recent work has served to emphasize the possible importance of electrosmosis as a factor involved in the equilibria between vacuoles of plant cells and the outside medium. There is still, however, too little information regarding molecular structure of cell membranes and too little certainty regarding location of various metabolic reactions within the cell for any quantitative treatment to be possible.

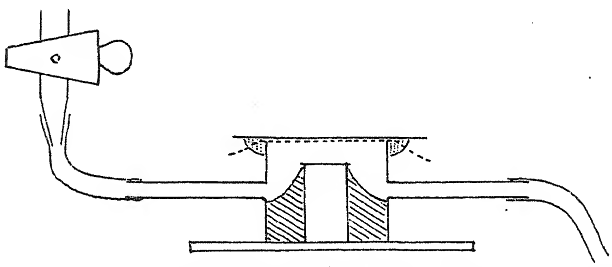

Fig. 1. Perfusion apparatus. Paraffin filling shaded; strip of tissue shown by dotted line.

It was thought possible that electrolyte and non-electrolyte plasmolysing agents might have rather different effects on the course of plasmolysis if, in fact, electrosmosis plays any considerable part in the water relations of the vacuole. Work carried out to test this point is quoted here as some of the results may be of interest, although no clear-cut answer to the problem originally posed has been obtained.

Experimental methods and materials

Sections or strips of tissue were mounted so that they could be perfused with any desired solution whilst any given cell or cells were kept under observation using an eyepiece micrometer to determine cell dimensions. Changes in size of the vacuole and protoplast were noted when the medium bathing the protoplast was changed. Some of the effects produced by change of the bathing liquid were readily predictable, others, such as the increase in volume of the vacuole when tissue is transferred from NaCl solutions to sucrose solutions of higher osmotic pressure, were more surprising and are dealt with here.

For a variety of reasons rapid transfer of solutions was wanted, and the apparatus which seemed to work best is illustrated in Fig. 1. A cylinder, as for a hanging-drop

culture, is cemented on to a slide, and most of the space inside is filled by a cylinder with an optical flat top (a glass tube with cover-slip cemented on to the top is satisfactory, mica tubes and covers were found to be even easier to construct): the strip of tissue is laid over the top and a cover-glass stuck on with lanoline: the space containing the bathing fluid is small and is streamlined with paraffin wax filling as indicated; this was found necessary in order to ensure quick replacement of one liquid by the second liquid. In order to make such a change the second bathing fluid is run through from a burette whilst the tissue is kept under observation.

Most of the work described here was done on the inner epidermis of onion-bulb scales. The onions were grown from seed supplied as 'Ailsa Craig'. The bulbs were dormant at the time of the experiments.

Having examined the behaviour of protoplasts while still enclosed in their cell walls, it was then found desirable to investigate isolated protoplasts. These are easily obtained by plasmolysing a strip of onion epidermis in sucrose solution and cutting across at right angles to the long axis of the cells with sharp scissors; the protoplasts can then be got out of the opened cells either by squeezing with a micro-glass rod or in some cases by transferring the tissue to NaCl solutions. The mechanism of this latter method will be discussed when dealing with experimental results.

The isolated protoplasts are most easily transferred from one solution to another by sucking them from the first solution into micro-pipettes and then expelling them into the second solution.

Osmotic pressures of the various solutions used were determined cryoscopically and the values cited are the osmotic pressures at 0° C. We are assuming that a negligible error is introduced by treating solutions isotonic at 0° C. as still isotonic at 16–18° C. Osmotic pressures of non-electrolytes will be about 6·2% larger at this higher temperature, but, in the case of electrolytes, altered association of ions will make their osmotic pressures somewhat different from this.

EXPERIMENTAL DATA

Changes induced by rapid transfer from sucrose to salt solutions

In certain experiments strips of inner epidermis of dormant onion bulbs mounted in the apparatus described were perfused with KCl solutions of osmotic pressure 27·9 atm.: plasmolysis was almost complete after 40 min. and followed the expected course. Determinations relating to cell XLI are plotted graphically in Fig. 2 and illustrate this phenomenon. Vacuole volumes are plotted as ordinates, and times in minutes are shown as abscissae. In this particular case 70 min. after supply of 27·9 atm. KCl, the KCl solution was washed away and replaced with 31·6 atm. sucrose.

The effect of supply of a sucrose solution of higher osmotic pressure was not to cause shrinkage, as might have been expected, but rather a temporary swelling followed by a shrinkage of the vacuole which soon attained the same volume that had previously been attained when the cell was bathed with KCl. Transference back to the KCl produced converse effects; shrinkage followed by expansion to the 'equilibrium volume' occurred.

It will be noted that the same equilibrium volume of the vacuole was attained in solutions of different osmotic pressure. There was a period of 15–30 min. after transference from KCl to sucrose before the equilibrium volume was re-established; this

period of equilibration was about 10 min. following transference from sucrose to KCl. This particular cell was subjected to three more transfers into sucrose and back into KCl, the osmotic pressures being 31·6 and 27·9 atm. respectively in each case. The times of these transfers and various details are indicated in Fig. 2. It will be noted that the effects produced by the salt to sucrose transfers were greater and of longer duration than those produced by sucrose to salt transfers. The equilibrium volume of the vacuole remained almost constant during the 23 hr. of the experiment.

The behaviour of another similar cell treated at the same time is shown in Fig. 3. The scale of this figure has been chosen so as to show rather more clearly details of the time course of this change of plasmolyticum effect.

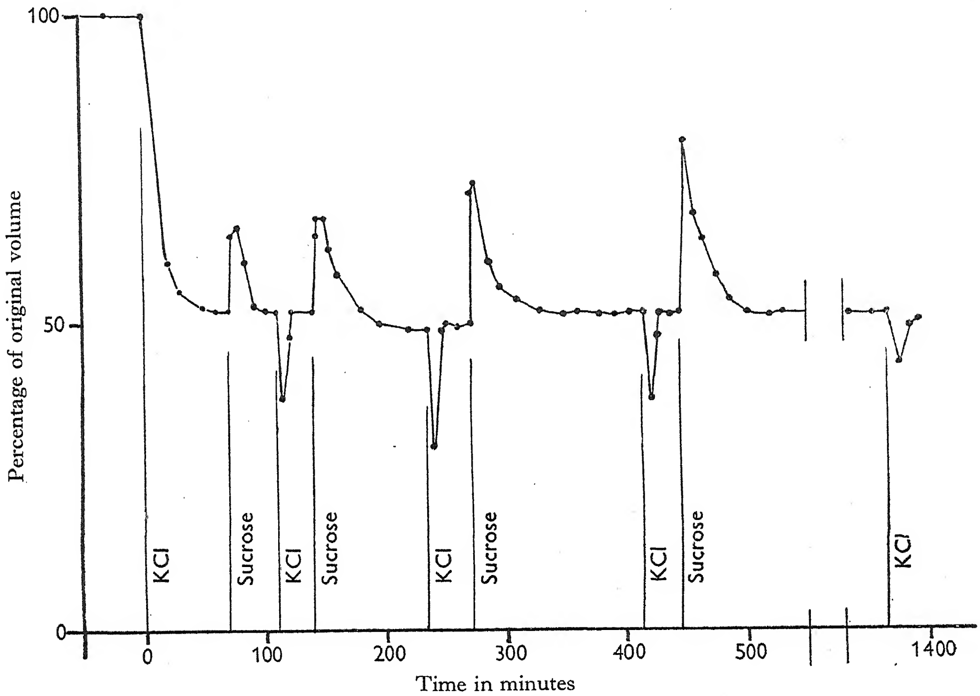

Fig. 2. Volume changes of cell XLI during successive exposures to 27·9 atm. KCl and 31·6 atm. sucrose. Ordinates show vacuole volumes as percentage of volume when immersed in water; abscissae times in minutes.

In a number of other experiments similar results were obtained, and in most cases the osmotic pressure of KCl required to bring the cell vacuole volume to a given value was about 10% lower than the osmotic pressure of sucrose required to bring it to the same equilibrium volume.

The effects brought about by other salts have been investigated. Salts of bi- and tri-valent cations cause the protoplast to take up a very irregular outline (concave plasmolysis), and measurements of volume changes under these circumstances are impossible. The plasmolysis form taken up in any plasmolyticum, sucrose and KCl included, is much influenced by the distance of the cell from the cut edge of the strip of epidermis. Cells close to the edge and thus presumably affected by wound stimuli more than the

more distant cells show a greater tendency to convex plasmolysis than the central cells of the strip.

Transference of a cell from sucrose or KCl to $CaCl_2$ results (except in the case of edge cells) in conversion of a spherical protoplast into an irregularly crumpled form. This is probably due to a change in volume coupled with increase in rigidity of external layers of the protoplast. The spherical form is regained on transfer back to sucrose.

Occasionally edge cells were found in which the convex plasmolysis form was retained even in $CaCl_2$ or $LaCl_3$, but one recognized that such cells had probably received gross wound stimuli. Behaviour of such a cell is shown in Fig. 4. It will be noted that considerable shrinkage occurred on transfer from 35·1 atm. sucrose to 28 atm. solutions of NaCl, $CaCl_2$ and $LaCl_3$, coupled with corresponding swelling when the reverse transfers

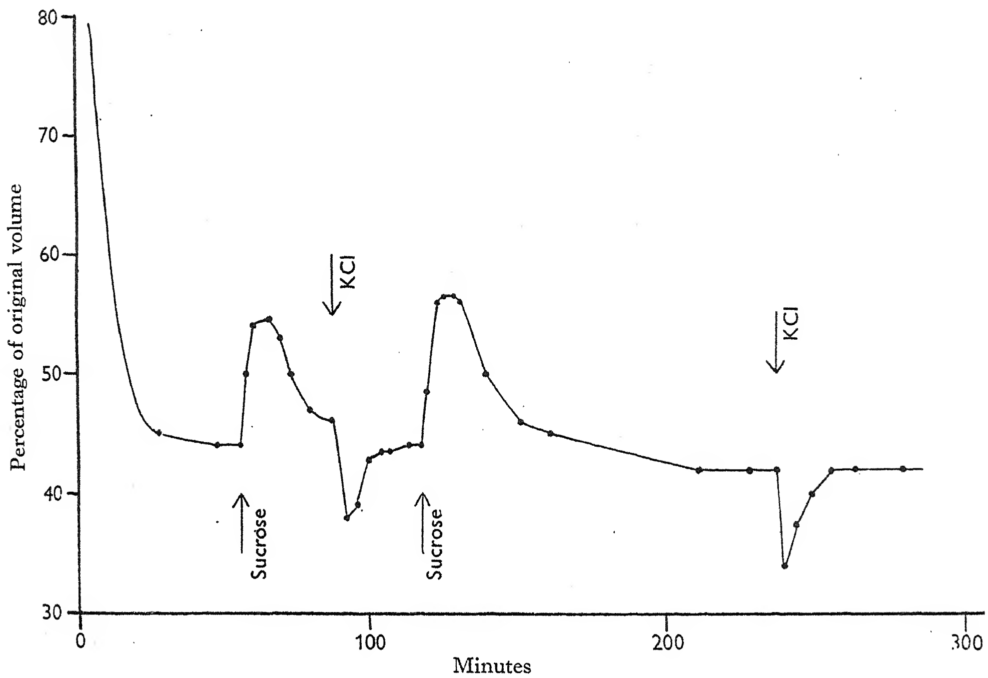

Fig. 3. Data for cell XLII similar to those of Fig. 2.

were carried out. The initial shrinkage on transfer to NaCl was large and was followed by a fairly rapid recovery to the equilibrium volume; the very rapid initial shrinkage was completed within 2 min. and the recoveries took 3–10 min. The protoplast had the appearance of a collapsing toy rubber balloon during the shrinkage phase; it then rounded itself and became smooth during the recovery phase.

We thought at first that these striking changes in vacuole volume resulting from a change in the bathing liquid were due to changes in osmotic pressure of the liquid in the space between wall and plasmolysed protoplast. The composition of the liquid in this space (termed shortly the intramural space) is controlled by the rates of diffusion of the plasmolytica across the cell wall: thus when a cell in equilibrium with 28 atm. KCl is transferred to 28 atm. sucrose, KCl will diffuse out of the intramural space more quickly than sucrose will diffuse in, and the osmotic pressure of the liquid in the space

will be reduced and the protoplast and vacuole will start recovering from plasmolysis. Finally, as equilibrium between the intramural space and the sucrose solution outside becomes established the protoplast replasmolyses.

This hypothesis, the validity of which will be dealt with in the general discussion, caused us to investigate the behaviour of isolated protoplasts.

Behaviour of isolated protoplasts

Epidermal strips were plasmolysed with 28 atm. KCl and were cut across the long axis of the cells with scissors; cells along the edge of the strip were cut open and in many of them the protoplasts were cut through and destroyed, but in other cases they were left inside the opened cell in a fairly undamaged condition. They could be pressed

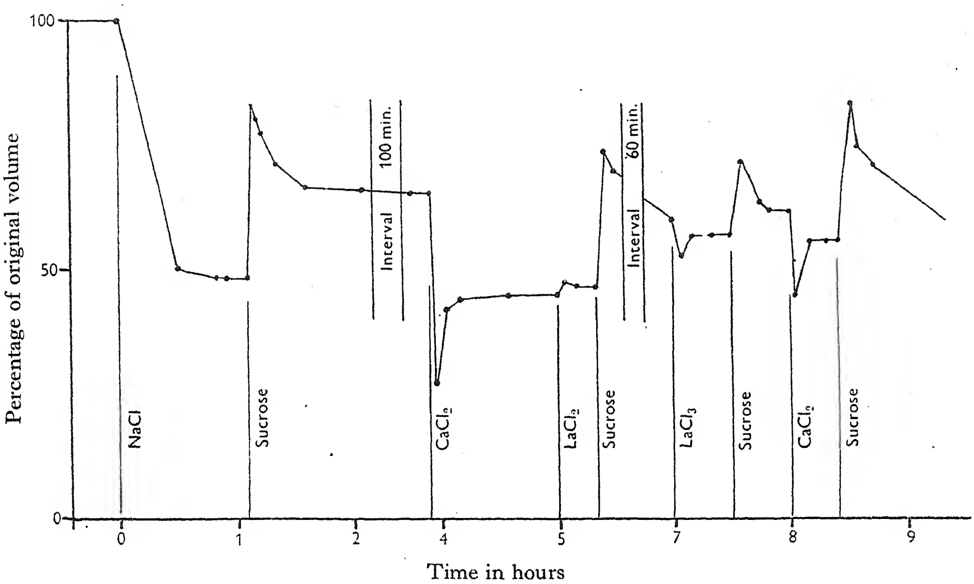

Fig. 4. Data for cell LXXXVII similar to those of Fig. 2 except that the following solutions were used: sucrose 35·1, NaCl 28, $CaCl_2$ 29, $LaCl_3$ 27·9 atm. Abscissae show time in hours.

out by gently rolling a fine glass rod over the tissue towards the cut surface. The isolated protoplasts at once took up a spherical form. Such protoplasts are very fragile and readily 'burst' in the course of manipulation.

The bursting looks very like the bursting of a rubber balloon, and though burstings are more frequent when the protoplasts are much distended they do occur frequently in considerably shrunken protoplasts; vacuolar contents of course escape on bursting, and there is left a solid shrunken mass consisting presumably of the two ectoplasts or plasmagels bounding the inner and outer plasmatic membranes. The fate of the central plasmasol is much less certain, though it seems likely that coagulation and precipitation on the plasmagel layers occurs.

Occasionally the external plasmagel bursts, and a solid shrunken mass consisting of this layer and possibly of coagulated parts of the plasmasol separates off from the so-called tonoplast which remains surrounding the vacuole. We have examined the changes

induced by transfer from salt to sugar solution of both complete isolated protoplasts and of isolated tonoplasts.

The transfers were done by sucking the protoplast into the drawn-out tip of a narrow tube with as little as possible of the bathing liquid and then blowing it into a large volume of the second liquid. Protoplasts were often found to burst if they touched the side of the glass micro-pipette.

The behaviour of a typical isolated protoplast (cell no. CXLIII) is given in Fig. 5. The volume changes following transfers from 28 atm. sucrose to 28 atm. KCl and back again were quite considerable and followed a course very similar to that found when the protoplast is enclosed inside its cell wall. It may be noted that isolated protoplasts often burst on transfer from KCl to sucrose, possibly because the rapid initial swelling tears the surface layers of the cell.

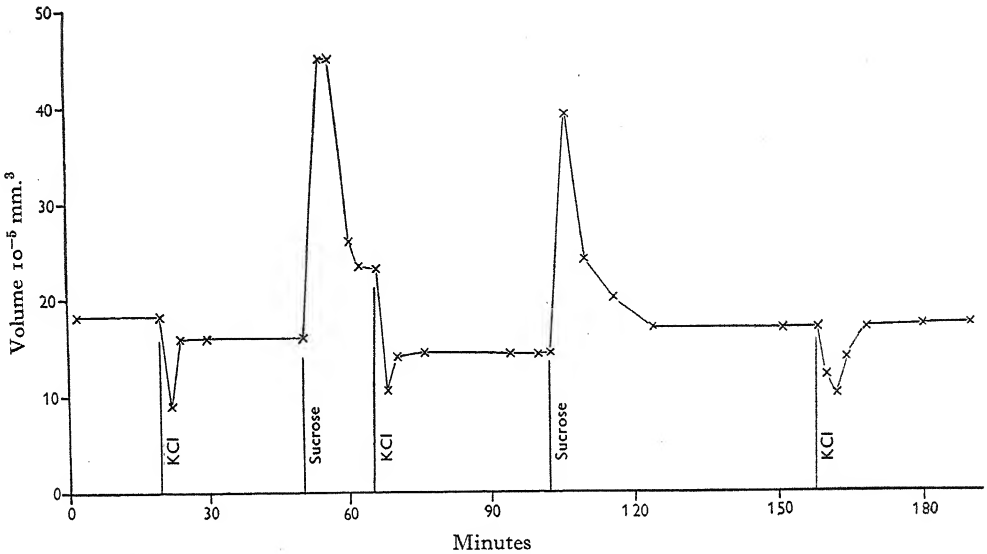

Fig. 5. Volume changes of isolated protoplast CXLIII following transfers from sucrose to KCl and vice versa. Osmotic pressure of both 28 atm. Volumes shown as ordinates are given as cu.mm. $\times 10^{-5}$. Times shown in minutes as abscissae are recorded with zero time arbitrarily fixed.

Behaviour of partially enclosed protoplasts

Strips of epidermis plasmolysed and cut across as described show, along the cut edge, cells in the states represented in the diagram in Fig. 6.

Protoplasts may be exposed with an intramural space behind as in cell *ABC*, or they may be so plasmolysed that there is almost no space behind as in cell *D* or, of course, the protoplasts may be lost as in other cells shown, or small fragments only may be present. Let us assume that the strip represented in Fig. 6 is bathed with and in equilibrium with 20 atm. sucrose. On transfer to 20 atm. KCl all the protoplasts shrink rapidly, i.e. the length *BC* decreases. The dimension *AB* increases at the same time as one would expect.

What is of special interest for understanding of the mechanism of these effects is the direction of movement of the external face *C* of the protoplast. In many cases this

moved outwards so that the whole protoplast, whilst shrinking, travelled slowly to the right like a piston being pushed out of a cylinder; sometimes when the protoplast was near the cut edge and the intramural space behind was large, the protoplasts were pushed right out into the surrounding liquid, but more usually they only moved a short distance towards the cut edge of the cell. This piston effect did not invariably occur; sometimes the external face of the protoplast moved inwards when transfer from sucrose to KCl was made.

Discussion

It seems certain that osmotic pressure changes of the liquid enclosed in the intramural spaces must occur when one plasmolyticum is changed for a different plasmolyticum of the same osmotic pressure. We have not sufficient data regarding the permeability of these cell walls to water, KCl or other salts and sucrose to be able to calculate the changes in osmotic pressure accurately. One can, however, obtain indications of the

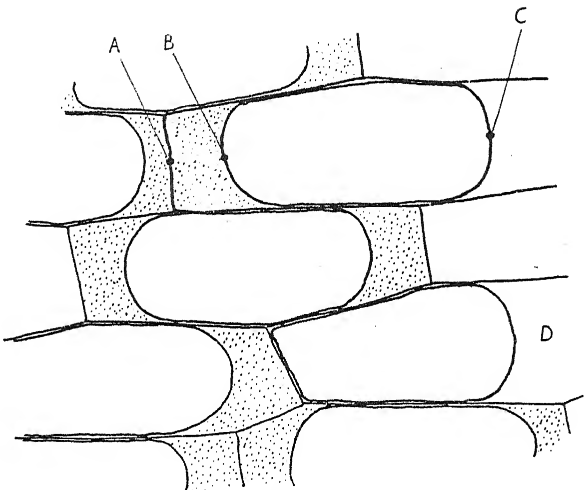

Fig. 6. Protoplasts at the edge of a cut strip of epidermis. The cut edge is on the right of the figure so that the protoplast surfaces *C* and *D* are directly exposed to external plasmolyticum. Intramural spaces are dotted.

order of magnitude of the osmotic pressure changes and their time course under certain limiting conditions. One could treat, for simplicity, the intramural space as a sphere or cube of given composition surrounded initially by infinite space of different composition and assume that the boundary between the two phases exercised no effect on the values of the diffusion constants of the solutes in these two aqueous phases. It became apparent that spheres of the size of our cells should approach equilibrium much more quickly than is observed to be the case with onion epidermis cells. The simplest explanation of the slow equilibration actually observed is that the cell-wall boundary between the two phases greatly retards diffusion; that this is in fact the case is made fairly clear by the work of Skene (1943) and the earlier work of Hofler (1930). Skene estimates the retardation of diffusion of sucrose in beet cell walls as 80-fold and of KCl as 40-fold.

If we assume a diffusion constant in the wall as low as 1% of that in free aqueous solution we can, for ease in calculation, assume instantaneous mixing of solute in both inner and outer phases, and that all the diffusion resistance is located in the cell walls.

The following relation then holds for outward diffusion from the intramural space containing solution into an infinite mass of pure solvent:

$$\frac{dx}{dt}=kS\frac{dC}{dl},$$

whence
$$\frac{vdC}{dt}=kS\frac{dC}{dl}\quad\text{or}\quad\frac{dC}{dt}=\frac{kS}{v}\frac{C}{l_m},$$

where x is the quantity and C the molar concentration of the substance diffusing, k the diffusion constant, v the volume and S the surface area of the cell wall, l_m the length of the diffusion path in the membrane (i.e. the thickness), and t the time. Hence

$$t=\frac{vl_m}{kS}\ln\frac{C_0}{C_t}=2{\cdot}3\,\frac{vl_m}{kS}\log_{10}\frac{C_0}{C_t},$$

where C_0 and C_t are the internal molar concentrations at the start of the diffusion process and that remaining after time t, respectively.

The dimensions of the cell, v, S and l_m, are constant and so, for any one substance, is k. For preliminary rough calculation, we may take the onion cell to have the dimensions of a cube with sides 0·01 cm. long; hence $v=10^{-6}$ c.c., $S=6\times10^{-4}$ cm.^{2} and $l_m=10^{-4}$ cm. In addition k_{sucrose} and k_{KCl} are 0·4 and $1{\cdot}62\times10^{-5}$ respectively in free aqueous solutions of the concentration range we are concerned with here. We are taking the value of k_{sucrose} in the cell wall as $0{\cdot}4\times10^{-7}$, and using these values can calculate the change in osmotic pressure with time of a sucrose solution enclosed in an intramural space of these dimensions when surrounded by a sucrose-free solution (assuming osmotic pressure to be proportional to concentration).

A similar expression can be used to calculate the change of internal osmotic pressure with time when the initial internal osmotic pressure is zero and the cell is surrounded by a solution of very large volume and thus of constant osmotic pressure.

In this case
$$t=2{\cdot}3\,\frac{vl_m}{k'S}\log_{10}\frac{C'_0}{C'_0-C'_t}.$$

A cell of the dimensions given, initially full of sucrose solution having osmotic pressure of 100 units, immersed in KCl solution of the same osmotic pressure will lose sucrose to the external solution and gain KCl from the external solution. The partial osmotic pressure of the cell contents due to sucrose calculated as described is given by the curve labelled sucrose in Fig. 7. The partial pressure due to KCl is given by the curve labelled KCl; in calculating this, the value chosen for the diffusion constant of KCl in the cell wall was 0·02 times the free aqueous diffusion constant. The sum of the partial pressure due to sucrose and KCl is given as the curve labelled 'sum'.

It will be seen that the maximum osmotic pressure is attained between 1·0 and 1·5 sec. after zero hour, and the maximum value is 67% above the initial and final equilibrium values.

These times depend, of course, on the values assigned to the constants. If the retardation of diffusion due to the wall is a hundred times greater than the values chosen by us on the basis of Skene's results, the time scale will be extended a hundred times and the maximum osmotic pressure would be found at about 130 sec. after zero hour and

the internal osmotic pressure would return to within 5% of the initial value after about 20 min.*

Such marked retardations of diffusion by the cell wall seem a little improbable, but it will be noted that the shape of the curve of change-of-plasmolyticum effect experimentally found is very similar to that of the summed curve of Fig. 7.

The whole change of plasmolyticum effect ought to be completed in about 15–20 sec. on the basis of this hypothesis, and taking retardations of diffusion close to those found by Skene. The much slower experimentally observed time course together with other features of the data fail to support this simple view of the phenomenon.

It can be readily shown that when a cell initially full of KCl is transferred to isotonic sucrose changes in the osmotic pressure of the intramural space occur which are, so to

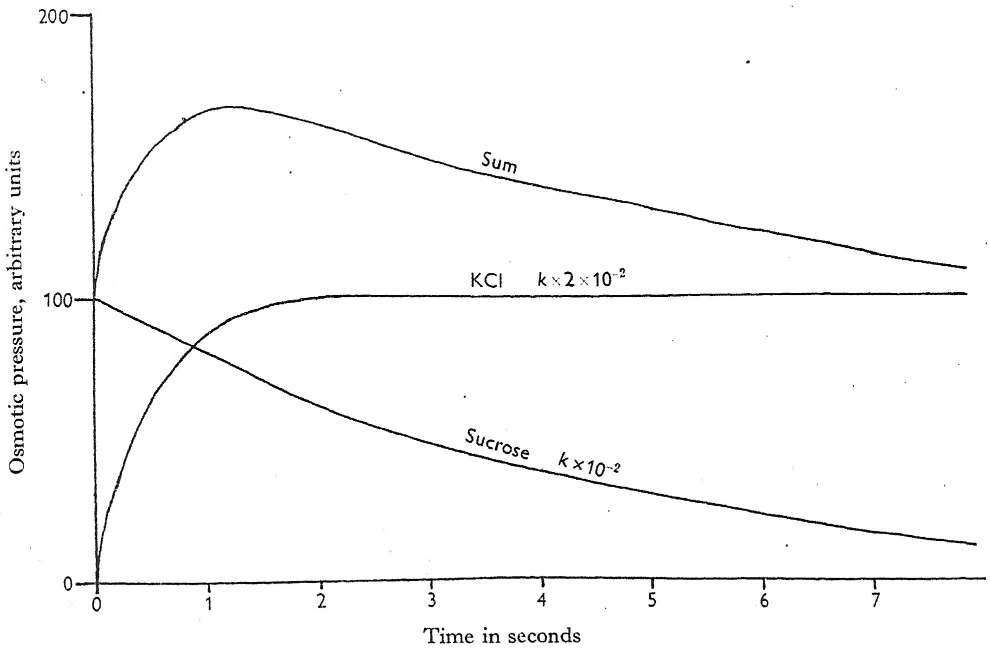

Fig. 7. Time course of osmotic pressure changes inside a cube with side 0·1 mm. long, initially full of sucrose and immersed in infinite volume of isotonic KCl. Further details and discussion in text.

speak, the mirror image of the changes occurring when the reverse transfer from sucrose to KCl is carried out. The actual data show, however, that the time course of swelling of the protoplast when KCl-to-sucrose exchange is made is some 5–8 times longer than that occurring after a sucrose-to-KCl exchange.

The changes in osmotic pressure of the intramural spaces which would be required to bring about the actual contractions and expansions of the protoplasts which have been observed in different experiments are sometimes considerable. They can be approximately deduced if one assumes a linear relation between osmotic pressure of intramural space and volume of protoplast.

For example, cell XLI (see Fig. 2) showed a degree of plasmolysis equal to 0·49 in

* As the value chosen for v is about 20 times too large, in all probability the length of time for equilibration has been overestimated by this extent. Proper estimates of values of v, S and l_m are unobtainable, so we have deliberately overestimated the 'calculated' time of attainment of maximum osmotic pressure.

sucrose of 31·6 atm.; on transfer to 28 atm. KCl it shrank until the degree of plasmolysis was 0·30. To bring about this shrinkage simply by increase in osmotic pressure of the liquid in the intramural space, it would be necessary for this osmotic pressure to be raised to approximately 52 atm. by inward diffusion of KCl. Cell LXXXVII similarly had a degree of plasmolysis equal to 0·52 in 35·1 atm. sucrose, and on transfer to 28 atm. NaCl shrank till the degree of plasmolysis was 0·27; this would require a rise of osmotic pressure of the intramural space to about 68 atm.

The second of these rises in osmotic pressure is bigger than can be accounted for by the hypothesis in the form presented above. If, however, the diffusion constant of sucrose (k) is decreased by the wall to a much greater extent than the diffusion constant of KCl (k'), one could approach to a limiting condition where the maximum internal osmotic pressure was nearly the sum of the osmotic pressure of the sucrose + KCl. Even this condition does not explain many of the contractions observed. Cell LXXXVII, for example, which has just been referred to, would have required an intramural osmotic pressure of at least 68 atm. to account for the contraction observed. Since the sucrose and KCl plasmolytica had 35·1 and 28 atm. osmotic pressure respectively, an intramural osmotic pressure above 35·1 + 28 (= 63 atm.) is impossible.

The behaviour of cut open cells seems finally to eliminate the possibility that this very slow diffusion in the cell walls as postulated really occurs. A cell, such as *ABC* in Fig. 6, would tend to develop a high osmotic pressure in the intramural space *AB* which would persist for several minutes if the wall had the necessary impermeability to account for the time course of the observed protoplast shrinkages. The development of such pressures would blow the protoplast out of the cell.

This does not happen; the protoplast moves along slightly for about 30–60 sec., which would be expected if the diffusion coefficients in the wall were not much smaller (say 1%) than in aqueous solution.

Finally, the fact that isolated protoplasts behave in a manner very similar to those enclosed in cell walls strongly suggests that diffusion effects due to the wall play a secondary part in promoting these changes of plasmolyticum effects.

We incline, then, to an explanation based on electrosmotic phenomena. Most natural membranes, such as those we are concerned with here, are negatively charged and, consequently, when electrosmosis is induced by application of a P.D. water flows to the negative electrode as shown in Fig. 8*a*. Membranes of this type are relatively impermeable to anions; thus the mobility of K^+ is greater than that of Cl^- in such a membrane, though their mobilities are nearly equal in water.

If a protoplast plasmolysed in sucrose is transferred to isotonic KCl, KCl may be expected to diffuse into it, and, owing to the greater mobility of K^+ than Cl^- in the membrane, the inside of the membrane will become positively charged relatively to the outside. Electrosmosis of the water in the membrane resulting from this membrane potential will cause flow of water outwards; it is most simple to look upon the effect of the isotonic KCl as due to the sum of its osmotic action (which equals that of the sucrose) and of this electrosmotic effect. One expects on this view passage of water outwards, i.e. shrinkage of protoplast or vacuole, when the cell is transferred from sucrose to isotonic KCl (see Fig. 8*b*).

When diffusion establishes equilibrium between KCl inside the protoplast and the liquid bathing it, the membrane potential due to KCl will fall to zero and the extra

electrosmotic effect due to KCl diffusion will vanish. One may note, in parentheses, that, if the cell in the course of its metabolism consumes KCl by any process, then this equilibrium will not be established and the possibility of slow continued inward leakage exists; such a continued entry of KCl would, on the basis of this hypothesis, result in a maintained and permanent shrinkage of the protoplast which would be expected to take up a smaller volume in KCl than in isotonic sucrose. This condition was observed with many of the cells examined by us.

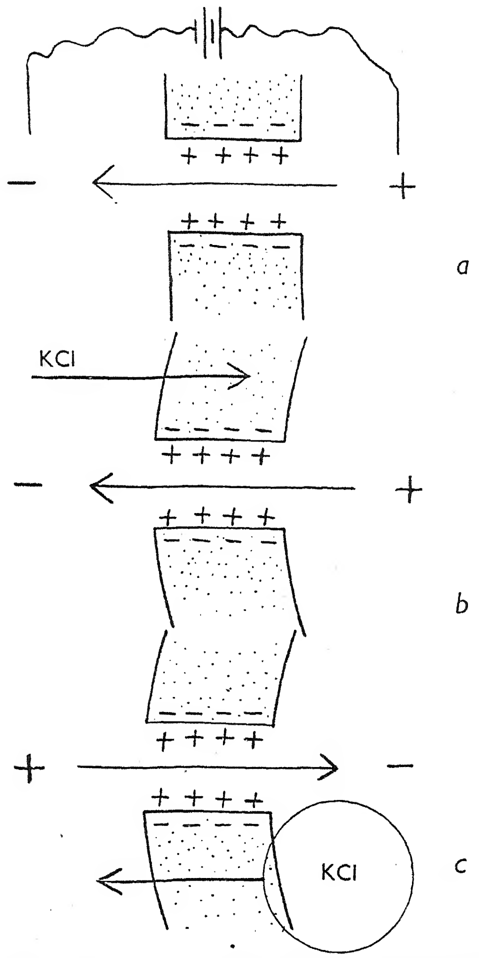

Fig. 8. Electrosmosis through membranes. (*a*) Under influence of an externally applied P.D. (*b*) Possible behaviour of protoplast when immersed in KCl solution; KCl diffuses inwards, i.e. to the right. (*c*) Possible behaviour on transfer back to sucrose showing KCl diffusing out. Arrows in the centres of pores indicate direction of flow of water due to electrosmosis.

Transfer back from KCl to isotonic sucrose will produce the converse reactions; diffusion of KCl outwards will cause the outside of the cell membrane to be positive relative to the inside, and as the system approaches equilibrium this membrane potential will drop towards zero. Associated with these membrane potential changes one would expect an initial electrosmotic pressure sending water into the protoplast which would then fall off to zero. These expectations agree broadly with the actual experimental findings.

We present the view, as an initial working hypothesis, that these change-of-plasmolyticum effects are due to these rather simple electrosmotically induced diffusion phenomena. Coincident with the swelling and shrinkage noted there occur almost certainly metabolic changes which may be caused by changes in the vacuolar surface or which may possibly themselves be one of the causative factors affecting the vacuole volume.

These metabolic changes have not yet been studied by us in the case of onion epidermis tissue, though we have some data as yet unpublished on effects found when similar sugar to salt transfers are carried out on beetroot tissue. When beetroot tissue slices plasmolysed in 28 atm. sucrose are transferred to 28 atm. KCl, there is a marked temporary enhancement of respiration lasting about 30 min. with R.Q. between 1·3 and 2. The reverse transfer causes an enhancement of respiration of similar time course but with an R.Q. less than unity.

The full significance of these metabolic changes is not yet clear, nor do we know whether there are similarities in metabolism of dormant onion and dormant beet tissue.

Volume changes similar to those found in onion epidermis were found in beetroot tissue and in beet-leaf tissue, also in leaf tissues of *Tradescantia*; we have as yet no idea of the extent of occurrence of this phenomenon; the effect is much more strongly marked in onion than in the other tissues just mentioned above. That this change of plasmolyticum effect has not already been widely observed and discussed has surprised us, and one can only conclude that this particular technique for comparison of tonicity of solutions has not been used.

SUMMARY

1. Transfer of onion epidermis cells plasmolysed in sucrose solutions to isotonic solutions of NaCl, KCl, $CaCl_2$ or $LaCl_3$ causes an almost instantaneous contraction in volume of the vacuole to about half the former plasmolysed volume in the case of K and Na and to a less marked extent with the other salts; in a short time (10–20 min.) the contracted vacuole expands again recovering to the 'equilibrium' plasmolysed volume. Transfer from the salt back to isotonic sugar is followed by comparable volume changes in the opposite direction; a very rapid increase in volume of the vacuole occurs which is followed by recovery to the equilibrium plasmolysed volume; frequently the increase in volume following transfer from salt to isotonic sugar has been so great that the protoplast has completely filled the space inside the cell wall and has then quickly replasmolysed. The rapid increase in volume often causes bursting of the protoplast.

2. Cut open cells (Fig. 6) can act like cylinders with the plasmolysed protoplasts playing the part of pistons; any large osmotic pressure developed in the cylinder behind the piston would naturally force the piston out rapidly; in fact, only small movements are observed, and from this and from calculations dealt with in the discussion we have concluded that the volume changes following change of plasmolyticum are not caused entirely by change in osmotic pressure of the liquid in the intramural space.

3. Isolated protoplasts also show similar volume changes when transferred from electrolyte to non-electrolyte plasmolytica, and this further suggests that the phenomenon is due to the structure or activity of the protoplast rather than to diffusion effects produced by the cell wall.

4. Electrosmosis is tentatively suggested as the cause of the observed volume changes.

Our thanks are due to Drs Prideaux and Davy with whom we have discussed the calculation of the intramural osmotic pressures and who suggested the simplified treatment presented above, and who provided the more rigid treatment that we have not reproduced in detail here.

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THE IRON-MANGANESE BALANCE AND ITS EFFECT ON THE GROWTH AND DEVELOPMENT OF PLANTS

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It has been shown in recent years that manganese, zinc, copper, boron and molybdenum are essential for the normal growth and development of certain plants. Little attention, however, has been given to the effect of the proportions of these minor elements relative to those of the other recognized mineral nutrients. Recently, Shive (1941) emphasized the importance of the balance between the available iron and manganese in the nutrient substrate and between the active concentrations of these elements in the plant tissues. In 1942, Somers & Shive stated that for the normal growth of soya bean the ratio of the concentrations of available iron and manganese must be around 2·0 both in the culture medium and in the tissues. Pathological symptoms of manganese deficiency appeared if the ratio of iron to manganese was greater than 2·0, but if it was less than 2·0 the symptoms of iron deficiency appeared. This work and unpublished data obtained by the author with oat plants indicate the importance of the iron-manganese balance in plant metabolism. The purpose of this paper is to review the literature on this special aspect of plant nutrition.

As far back as 1848 Salm-Horstmar carried out an investigation with oat plants by varying the proportions of iron and manganese in a nutrient substrate. The results of this investigation were published in 1849; I have not found any reference to them in subsequent literature.

Salm-Horstmar (1849) described a plant in his Exp. 20 in the following terms: 'The leaves were 12 in. long and ½ in. broad, a good dark green in colour, and were normal as regards their rigidity and roughness, but after the development of the fourth leaf there appeared in the middle of all the subsequent leaves, dry spots of a grey-green colour.' In 1851 he described a plant in his 16th experiment by saying: 'When the fourth leaf was only partially developed, there appeared on the third leaf a brownish spot; this region was dried up.' This spot, and others like it that appeared on the third, fifth and sixth leaves, resembled those described in the first quotation. These two descriptions are probably the first recorded descriptions of manganese deficiency.

In Exp. 20 of the 1849 paper the symptoms described above appeared in a culture supplied with iron but without manganese. In Exp. 21 he used less iron and no manganese in the nutrient medium, with the result that only one leaf of the plant had a necrotic spot in the middle of its blade. The conclusion was that the concentration of iron in Exp. 20 (0·1 g. Eisenoxydul enthaltendes Eisenoxyd) was too great, causing dry patches of grey-green colour to appear, while in Exp. 21 (0·01 g. Eisenoxydul haltiges Eisenoxyd) the lower iron level had a less detrimental effect. When iron and manganese were supplied, as in Exps. 23 and 24, satisfactory growth and freedom from symptoms of grey speck were obtained, but if iron was omitted a chlorotic plant was produced (Exp. 25). The quantitative data are summarized in Table 1.

In 1851, Salm-Horstmar described further experiments with oat plants grown in sand culture. Here again he produced what I believe to be grey speck of oats in his 16th experiment (see quotation above), the nutrient substrate of which included iron but no manganese. With iron and manganese in the culture medium (Exp. 19) a plant free from the symptoms was produced, but with less iron and the same quantity of manganese (Exp. 20) the plant was chlorotic, a condition he attributes to the diminution of iron. In his conclusions to these experiments Salm-Horstmar states 'that before the formation of the fruits, manganese was not necessary to the oat plant when there was not too much iron in the culture solution'. Excess iron appeared to render manganese necessary for growth. Manganese, he states, will always be necessary for the plant in all soils where the iron level is above 1 : 100 and where iron is in contact with humus.

There is therefore in this early work evidence that iron influences the onset of manganese deficiency symptoms, particularly when humus is present, and that manganese in the absence of iron, or with little iron, may be the toxic agent bringing about iron chlorosis.

Loew & Sawa (1902), Aso (1902) and Fukutome (1904), working with various species, all observed manganese toxicity which was relieved by the addition of ferrous sulphate to the nutrient medium. A chlorosis of peas, barley and soya beans was observed by

Table 1 (after Salm-Horstmar, 1849)

Exp.	Treatment	Dry weight in g.	Height in in.
20	With Fe, no Mn	0·40	13
21	Less Fe, no Mn	0·49	24
23	With Fe and Mn	1·09	14
24	With Fe and Mn	1·29	26
25	No Fe with Mn	0·57	12

Loew & Sawa when the medium contained more than 0·02% manganese sulphate. Aso (1902), working with radish, barley, wheat and peas, observed that iron not only counteracted the development of the chlorosis caused by manganese but also depressed the stimulatory effect produced by 0·002% manganese sulphate. Fukutome (1904), working with flax, observed that the toxic effect of manganese chloride was overcome by ferrous sulphate. Brenchley (1910) found that the growth of barley was retarded when manganese sulphate was used in concentrations greater than 1 : 100,000 in the culture medium.

Pugliese (1913) grew grain (cereal species) in water culture using Knop's solution, to which were added varying amounts of ferrous sulphate and manganese salts. Manganese nitrate in concentrations greater than 0·05 g./l. was detrimental in the absence of iron but was stimulatory if iron was present as ferrous sulphate in concentrations between 0·07 and 0·15 g./l. He concluded, therefore, that in the presence of iron the plants could tolerate very much larger doses of manganese.

In 1916, Tottingham & Beck grew wheat in a Knop's solution minus ferric phosphate. They found that when iron (as ferric chloride) and manganese (as manganese chloride) were presented in low concentration ($M/100,000$) the manganese depressed the stimulating effect of iron, while at a higher concentration ($M/1000$) the iron depressed the stimulatory effect of manganese. At the low plane of supply manganese caused chlorosis in

the presence of iron, and they suggested that manganese interfered with the role of iron in the formation of chlorophyll.

The relation of iron and manganese to the growth of pineapples on certain Hawaiian soils was the subject of numerous papers by Kelley, Wilcox and Johnson. Kelley (1909) described a chlorosis of pineapples which was associated with a high manganese level in the soil. The black manganiferous soil on which the chlorotic pineapples were produced contained 0·733% Mn_3O_4, while the red soil producing a healthy crop contained only 0·02% Mn_3O_4 when estimated in a 1% citric acid extract. In 1912 he found large quantities of manganese in plants grown on the manganiferous soil. After making a comprehensive analysis of the plants for the various mineral constituents, Kelley observed a disturbance of the mineral balance in chlorotic plants. The lime percentage was increased while the absorption of magnesia and phosphoric acid was decreased. From this evidence Kelley states that the effects of manganese are probably indirect, and the toxic effects observed are brought about mainly by the disturbed mineral balance.

Table 2 (after Johnson, 1917). *Showing the iron (as* Fe_2O_3*) uptake of various species of plants grown on normal and manganiferous soils. The iron uptake from normal soil is regarded as* 1·0

	Iron uptake from manganiferous soil
A. Plants affected by manganese toxicity:	
Paspulum orbiculare	0·26
Peanut leaves	0·54
Pineapple leaves 5 months old	0·73
Sugar cane	0·72
Broom-corn leaves	0·81
Cowpea vine	0·84
Corn stove	0·87
B. Plants not affected by manganese toxicity:	
Waltheria americana leaves	1·20
Crotolaria	2·38
Guava leaves	6·67

Johnson (1917) asserts that there is no possible correlation between the toxicity symptoms (chlorosis) and the individual ash constituents. In the case of iron, however, he observed a depression of iron assimilation in those plants to which the manganiferous soil was toxic, while an increased iron assimilation was observed in plants not affected by the soil (see Table 2).

The occurrence of the toxicity symptoms could be controlled by a ferrous sulphate spray.

Gile (1916) pointed out several differences between the chlorosis of pineapples on Hawaiian soils and the chlorosis found near Porto Rico. His conclusions were that the manganese chlorosis of Hawaii was due in part to a deficiency of iron in the plant, induced by the action of manganese, while the lime-induced chlorosis of Porto Rico was merely the result of a lack of iron in the plant, due to calcium carbonate diminishing the availability of iron in the soil. He did not, however, overlook the possibility that the two kinds of chlorosis might be the same.

McGeorge (1923, from Jacks & Scherbatoff, 1934), after comparing Johnson's data with that of Kelley, came to the conclusion that 'the chlorosis of pineapples on manganese

soils is due to a greater assimilation of lime indirectly caused by the presence of large amounts of manganese in the soil, and that the principal physiological disturbance is the greater immobility of iron in the plant resulting from the excessive lime content of the leaves and stalk and the low rate of mobility of iron even in normal pineapple leaves'.

Rippel (1923) found that soluble manganese salts in water cultures of oat plants produced a chlorosis which was remedied by the addition of iron. The chlorotic and normal seedlings had the same iron content, and it was concluded that manganese did not prevent the uptake of iron but inhibited its action after absorption. This conclusion certainly falls into line with Shive's hypothesis (1941).

According to Bishop (1928), manganese does not cause a depression of the iron uptake (cf. Johnson, 1917) if the iron content of plants grown in a typical soil is taken as a standard (see Table 3).

It will be observed from these figures, however, that if the normal soil is not taken into consideration there is certainly a tendency for the amount of iron assimilated to be depressed in the sand cultures containing manganese, as compared with the cultures not supplied with manganese.

In *Citrus*, Haas (1932) found that excessive concentrations of manganese brought about chlorosis even though iron was added to the culture solution in similarly large

Table 3 (after Bishop, 1928). *Percentage iron* (*as* Fe_2O_3) *content of radish plants*

Reaction of substrate	Control no Mn	Treatment		
		5 p.p.m. Mn	10 p.p.m. Mn	Normal soil
Acid	0·092	0·088	0·087	0·093
Neutral	0·135	0·133	0·103	0·114

amounts. He also states that in most cases when manganese is deficient in *Citrus* leaves, less iron appears to be accumulated.

The most recent observations on the roles of iron and manganese in plant metabolism are those of Shive (1941), Somers, Gilbert & Shive (1942) and Somers and Shive (1942). These workers state that the theoretical explanation of the roles of manganese and iron in metabolic processes revolves round two facts: first, that the active functional iron is in the ferrous condition, and secondly, that the oxidizing potential of manganese is higher than that of iron. Ferric iron absorbed by plants is reduced within the cells to the ferrous state unless this reaction is prevented by some counter-reactant. If such a reactant is not present in the plant then a small amount of ferrous iron may be a powerful toxic agent causing symptoms of iron toxicity which are identical with manganese deficiency. If a strong oxidizing agent is present in the cells then the reduction of iron is somewhat restrained, or if ferrous iron is present some at least will be oxidized to the ferric state and probably will be precipitated in the form of a ferric organophosphate. They claim that manganese is an element which possesses the chemical characteristics necessary for such a theoretical system. Thus with a deficient supply of manganese ferrous iron will be dominant causing iron toxicity or manganese deficiency. On the other hand, if manganese is in excess then the iron will be immobilized in the tissues as a ferric organophosphate and the plants will show symptoms of manganese toxicity which are identical with iron deficiency. The optimum ratio of active iron to active

manganese in the plants (soya bean) must lie between 1·5 and 2·5 irrespective of the total amounts of these elements in the tissues. Experiments with oats by the author gave similar observational results to those seen by these workers. By increasing the concentration of iron in the nutrient medium oat plants showed a greater tendency to exhibit the symptoms of grey speck, and with the data available it is impossible to separate manganese deficiency from iron toxicity. Iron chlorosis is produced in oats by raising the manganese level in the nutrient medium, and if the iron concentration is raised more manganese must be added to bring about the symptoms. At this stage it is not possible to differentiate between iron deficiency and manganese toxicity.

Manganese deficiency seems to be correlated with a high level of mobile iron in the plant and in the substrate, since by decreasing the concentration of iron or by increasing the manganese in the substrate healthy plants can be grown. There is therefore the suggestion that manganese deficiency corresponds to iron toxicity. Iron chlorosis in certain cases is correlated with a high manganese concentration in the plant and in the nutrient medium and can be cured by reducing the manganese level in the substrate or by raising the iron content of the plants by spraying or by applications of iron salts to the soil or culture medium. There is, however, considerable evidence that the problem of chlorosis in the field is not always as simple as this. Lindner & Harley (1944) list four ways in which iron nutrition may be affected so as to bring about a chlorosis. These are: (1) true iron deficiency which occurs under experimental conditions and is not very prevalent in the field; (2) a disturbed phosphate/iron balance which causes a chlorosis; (3) a disturbed manganese/iron balance; and (4) lime-induced chlorosis. The last type of chlorosis is probably the most common in the field. Thus the occurrence of chlorosis in the field is a complex problem involving the interrelations of a number of elements, such as calcium, phosphorus, iron, manganese and magnesium.

The evidence summarized above suggests that the iron-manganese balance in the tissues and in the substrate is of great importance to the well-being of plants. The interrelationship of these two elements in plants and in the soil is probably just as important as the essentiality of either of them to plant growth.

There has been much speculation on the possible biochemical activity of iron and manganese in the plant. A brief review of the main points made in connexion with the functions of iron and manganese will not be out of place here.

There is evidence that manganese increases the activity of oxidizing enzymes in plants. The early work of Bertrand (1897) showed that laccase contained manganese and that the addition of soluble manganese salts to the oxidases greatly accelerated their oxygen-carrying power. Later in 1902, Loew & Sawa, and Aso, found that the sap extracts from chlorotic plants produced by applications of manganese sulphate were more vigorous oxidizing agents than those obtained from normal plants receiving less manganese. A similar observation was made by Kelley (1909), who showed that the yellow leaves of pineapples grown in the highly manganiferous soils of Hawaii contained a more active oxidase than normal healthy green leaves. Pugliese (1913) believed that manganese was bound up with various oxidation phenomena and that its function was concerned either directly as an oxidizing enzyme and accelerator of oxidizing enzymes or as an oxygen fixing agent in the soil. Furthermore, Pugliese found evidence which suggested that iron antagonized the action of manganese, alleviating its toxic effect and permitting the healthy growth of cereal species.

Many views have been put forward on the function of manganese in the plant. Kelley (1914) attributed a twofold function to manganese: '(1) it acts catalytically, increasing the oxidations in the soil and accelerating the autoxidations in plants; and (2) it tends to modify the absorption of lime and magnesia, perhaps partially replacing calcium from insoluble combinations, but especially, through a direct effect on the osmotic absorption of lime and magnesia, increasing the former and decreasing the latter'.

In 1923 and 1926, McHargue suggested that manganese had some function in the photosynthetic process and the formation of chlorophyll. In this connexion it must be noted that Miller (1933) showed that manganese-deficient plants were much lower in sugar than corresponding plants which had received small amounts of manganese. The results of his work therefore suggest that manganese plays an important part in sugar formation and sugar metabolism, either directly or indirectly.

Some workers have published evidence which suggests that the functions of iron and manganese are interrelated. For instance, in 1930, Hopkins suggested that manganese functions physiologically in an indirect manner by its action on the state of oxidation of iron. Manganese tends to control the ratio $Fe^{++} \rightleftharpoons Fe^{+++}$ in the culture medium and in the cell. He quotes an experiment in which the iron in a solution of ferric chloride was maintained in the ferric condition in the presence of sodium citrate by the addition of manganese. Further, he states that the reduction of iron by yeast cultures was prevented by the presence of manganese. In culture solutions containing manganese, ferric iron and sodium citrate a higher oxidation-reduction potential was developed than was obtained in the absence of manganese. On the basis of these observations he suggests that manganese must be present to insure the reoxidation of the iron after its reduction by the organism, and that too high a concentration of manganese results in a high proportion of ferric ions or prevents the reduction of this ferric iron by the organism. In this connexion it might be mentioned that Sideris & Kraus (1931) claimed that the toxicity of manganese is due to its chemical reaction with iron during which iron is rendered non-ionized and therefore inactive.

Lundegårdh (1939) produced evidence suggesting that manganese is concerned with the oxidation processes involved in respiration. The oxygen absorption of wheat roots was increased by the addition of manganese to 0·001 *M* solution of potassium chloride. The results of similar experiments with iron, as ferric citrate, suggest that iron reduces the oxygen absorption of wheat roots. He therefore concludes that manganese has a catalytic effect on the respiratory process while iron has not.

This review stresses the importance of the iron-manganese balance both in the plant itself and in the substrate in which it grows. The incidence of pathological symptoms of manganese deficiency and iron deficiency seems to be governed by the relative proportions of these elements. Further investigations are necessary on the effect of this balance on the growth of plants and the occurrence of pathological symptoms, so that the deficiency diseases concerned may be better understood. The fundamental problem of the functions of iron and manganese in plant metabolism has still to be solved.

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THE DIRECTION OF TORSION AND THE CHANGES OF SHAPE IN LEAVES FIXED DISTALLY OR COMPLETELY

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(With 11 figures in the text)

(1) The direction of torsion in leaves fixed distally

In a first paper on the torsions made by leaves in response to stimuli of light and gravity the writer (1942) explained why in order to interpret them it is important to determine in which direction the leaves twist if fixed distally and set free at the base, before being arranged on edge to be stimulated laterally. The experiments were made on detached leaves, and they showed that the stalks of various pinnate leaves fixed distally twisted in the normal or positive direction (that is, so as to bring the correct face uppermost by the shorter way round), but the pulvini of leaves of *Phaseolus multiflorus* and of leaflets of *Wistaria* in the abnormal or negative direction. But with the petioles of various simple leaves some of the results obtained at that time were not very clear, and consequently the writer was led to try a second method, described in the first part of a second paper (1945), which consisted in enabling leaves to twist at their bases not by cutting them off completely, but by reducing a basal zone of petiole to a thread-like conducting strip. With this second method some of the results obtained were puzzling, and in the first part of the present paper it will be shown that the second method is after all of no use for the purpose for which it was intended, since it often leads to torsions of a kind quite different from the true strophic responses.

The puzzling points in the results obtained with the second method were the following. First in *Lunaria biennis* and *Stachys silvatica* the petioles of leaves fixed distally usually made strong positive torsions, which often continued far beyond 90°, but in the earliest few experiments with this method, and in those only, they made negative torsions. Secondly the distal pulvini of leaves of *Phaseolus multiflorus* fixed distally made strong positive torsions, although in detached leaves they regularly made negative torsions.

It is, however, known that torsions which have nothing to do with the strophic responses may occur in previously curved geotropic organs if these are laid on one flank with the curvature in a horizontal plane and fixed at both ends. These torsions which have been described by Rawitscher (1932, p. 194), are brought about according to him in the following way. The lower side of the organ elongates the more through negative geotropism, but it cannot become the convex side of a curvature with one end pointing upwards, since both ends are fixed (see Fig. 1). So it shifts round towards the flank on which there is least resistance to its elongation, and that flank is the convex side of the previous curvature. Thereby a new side of the organ is brought into the lower position and stimulated geotropically, and so the process goes on.

The writer had often considered whether a similar process might have been occurring in the experiments with the second method on leaves fixed distally and arranged horizontally and on edge, and Prof. Rawitscher had indeed suggested to him in a letter that it might have done so: but at first he had thought that this was not possible, partly because in many of the species tested previously (1942), including *Phaseolus*, the geotropic curvatures of the detached leaves had been very small or nil, and partly because with the second method the thin basal zone was quite flexible. For this had made it seem that even if the geotropic curvature were sometimes big enough to pull taut the slack of the basal zone, the curvature would still continue without meeting resistance if the curved region bulged out downwards.

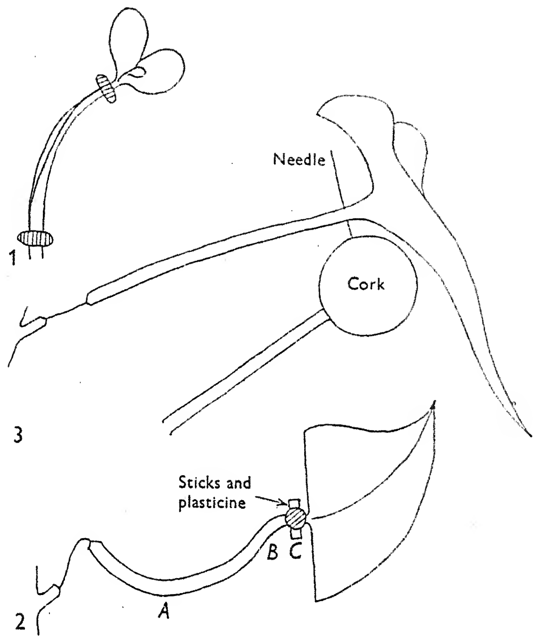


Fig. 1. A curved sunflower hypocotyl laid on one flank and fixed at both ends, after Rawitscher.
Fig. 2. For explanation see text.
Fig. 3. A leaf of *Lunaria biennis* mounted distally on a needle.

But this is not so, as can be made clear by means of Fig. 2, which represents diagrammatically such a leaf fixed at the distal end of the petiole, arranged on edge, and looked at from in front, so that its dorsal face is seen and the ends of the sticks that fix it. When the lower half of such a petiole elongates the more rapidly by negative geotropism, after some time the thread-like basal zone may be pulled taut and will then prevent the basal end from rising further. If this happens, a further elongation of the lower half cannot be accommodated without resistance by a curvature projecting downwards, such as is shown at A in Fig. 2, since the longitudinal direction of the petiole is firmly fixed at C where it is tied within a plasticine collar between sticks; and consequently the petiole cannot curve at A, unless it curves in the opposite direction at B so as to regain its fixed direction at C. Since therefore there is no physiological cause for an opposite curve at B, the tissues at B will resist any tendency to curve imposed upon them, and so the tendency to curve geotropically at A will meet with a resistance. Thus the conditions are present for a

torsion due to Rawitscher's two-end effect, and it may be expected that the lower half of the petiole will shift round towards the side on which there is the less resistance to its elongation. This side is likely to be the one occupied by the morphologically dorsal half of the petiole, since that half usually becomes convex by epinasty: and if so, then the direction of the torsion so caused will be normal or positive.

It is therefore possible after all that some part or all of the strong positive torsions obtained previously in various attached leaves fixed distally was caused in this way, and it is easy to test whether this was so by changing the method of distal fixation. For it was not really necessary for the purpose of the experiment to fix the *longitudinal directions* of the petioles at their distal ends, but only to prevent them from *twisting* at their distal ends, while leaving them free to twist at their basal ends: and if the longitudinal directions of the petioles in the vertical plane are not fixed at their distal ends, then there can be no torsions due to Rawitscher's two-end effect based on negative geotropism, since the

Table 1. *Torsions in degrees of petioles of* Lunaria biennis *fixed distally on needles*

Leaf	1 day	2 days	3 days	4 days
No. 1	−90	−110	−70	−120
2	−30	−80	−80	−90
3	−80	−210	−170	−90
4	−30	0	−20	−45

elongations of the lower sides will be accommodated without resistance by means of curvatures bulging out downwards. In order therefore to prevent the petioles from twisting at their distal ends without fixing their longitudinal directions, they were now fixed in the way shown in Fig. 3. A fine needle was passed transversely through the distal end of the petiole in the dorsiventral plane, and the point of the needle, when it came out through the ventral surface, was stuck into a cork mounted on a stick which had been pushed into the earth in the pot containing the plant. Then the pot was laid horizontal as before, with the leaf on edge so that it was stimulated laterally by gravity. Fig. 3 shows a leaf in this position as seen from above. With this arrangement the petiole was prevented from twisting at the distal end more than a very little, as was verified by testing it with the fingers, but it was quite free to change its longitudinal direction at that end in the vertical plane by swinging on the needle as a pivot. It was also found rather unexpectedly that the petiole was fairly free to change its direction in the horizontal plane at the distal end. At its basal end of course it could readily change its direction, since the basal cut zones were quite flexible.

Four young leaves of *Lunaria biennis* were tested with this modified method, and the results are shown in Table 1.

Thus the distal fixations on needles led at once to negative torsions similar to those which had previously been obtained in the first few experiments with *Lunaria biennis* and *Stachys silvatica*. The petioles also made strong geotropic curvatures ranging from 90 to 120°.

When now the notes of the previous experiments were read again, it was found that in those first few experiments with both species in which the torsions were negative, the petioles had been tied distally between two sticks without any plasticine collar, but that

in all the later experiments in which the torsions were all positive, a plasticine collar was first put round them. So the explanation of the previous negative torsions is probably that when the petioles were tied between sticks without plasticine, then by slipping slightly they were free to change their longitudinal directions at their distal ends, though not to twist, just as when they were mounted on needles, but that when plasticine was used they could not do so. However, for the purpose of allowing this change of longitudinal direction, the method of mounting on a needle is much more certain and better.

Two young leaves of *Viola odorata* also were tested with the petioles mounted distally on needles, since previously when fixed distally in plasticine collars the petioles of this species had all made very strong positive torsions. In both of these the torsions were at first negative, reaching -100 and $-80°$, though in the second leaf the torsion reversed at 3 days and went to $+250°$.

Four young leaves of *Phaseolus multiflorus* also were tested with the needles passed through them at the extreme distal ends of the distal pulvini. In this species the pulvini of leaves fixed distally with plasticine and attached at the base had made strong positive torsions, though they had regularly made negative torsions in detached leaves. When fixed distally on needles and attached at the base by the usual thin conducting strand they made either no torsions or very weak negative ones.

These results make it clear that some part at least of the very strong positive torsions obtained previously when leaves still attached at the base were fixed distally with plasticine and sticks was indeed due to Rawitscher's 'two-end' effect, so that the method is useless for determining the direction of geostrophic torsion in leaves fixed distally. The writer therefore much regrets that by introducing this method in place of the earlier method of testing detached leaves, he only made unnecessary confusion.

But whereas the method of testing attached leaves had failed, more consistent and satisfactory results were now obtained when detached simple leaves were tested, according to the original method. The leaves tested were those of *Lunaria biennis* and *Scrophularia verna*, and this time they were picked and set up on the evenings of sunny days, the idea being to test them while well nourished. They were of about half the final length and were fixed distally by being attached to glass supports by means of strips of plasticine passed round the distal ends of the petioles as before. They were placed horizontal with their blades on edge, and with the lowest part of the blade just dipping into a film of water on a plate. In order to let the water enter more easily, the extreme margin of the submerged part of the blade was cut off. The plates with the leaves were closely covered with bell-jars and were placed out of doors in overhead light but in the shade.

Twelve vigorous young leaves of *Lunaria* were tested in this way, and in all of them the petioles twisted positively. The torsions reached their maxima after times ranging from 14 to 48 hr., but mostly after less than 24 hr., the maxima in degrees being 90, 90, 50, 40, 30, 25, 25, 25, 20, 20, 15 and 8. At the same time the petioles made strong geonegative curves, sometimes of 80° or even more, and rather less strong epinastic curves.

Six young leaves of *Scrophularia verna* were tested in the same way, and in four of them the petioles made positive torsions which reached 40, 30, 25 and 15° in one or two days. Their curvatures did not exceed 30°. In the other two leaves the petioles failed to twist or curve.

Also in an earlier experiment seventeen young leaves of *Nepeta hederacea* were tested in a similar way except that they were picked in the morning. In all of them the petioles

twisted positively, except one which failed to twist. The sixteen torsions reached figures ranging from 40 to 10° in 1 or 2 days, the mean being 22°.

These results with detached simple leaves show that in these three species at least the direction of the genuine strophic torsion in the petioles of leaves fixed distally and stimulated in the edgewise position is positive. This was also shown in the first paper of this series (1942) to be the direction of strophic torsion in the petioles and rachises of pinnate leaves of four species, so that it is probably the general rule for petioles and rachises. On the other hand, in the pulvini of detached leaves of *Phaseolus* fixed distally the direction of torsion is negative, as was twice shown previously (1942, 1945), and so also it is in pulvini of *Wistaria* (1942). Thus the correct conclusions were those reached in the first paper (1942).

There remains indeed the question how to explain the negative torsions which, as is here reported, were made by petioles of *Lunaria* when attached at the base by the usual thin conducting strand and mounted distally on needles, and also previously when the petioles were fixed distally between sticks but without plasticine. But since the experiments with detached leaves make it clear that the direction of genuine strophic torsion in distally fixed petioles of this species and others is positive, these negative torsions in petioles of attached leaves rather lose their interest. It may, however, be mentioned that in some species the direction of torsion in leaves attached by a thin strand at the base is positive, even when the petioles are mounted distally on needles and are quite free to swing on them. For in three young leaves of *Sambucus nigra* so treated, and in one of *Malva rotundifolia* the petioles made positive torsions. These were probably genuine strophic responses.

(2) The changes of shape in petioles stimulated in constraint

Since the positive torsions of petioles and rachises fixed distally are favourable to the transverse growth hypothesis of Rawitscher (1932, p. 203), as was explained previously (1942), the writer has twice reported experiments devised to test this hypothesis further (1942, 1945). In these experiments petioles were stimulated on edge for many days while mechanically prevented from twisting as wholes in response, and were then examined in transverse sections to see whether they had changed their shapes in ways favourable to the hypothesis. The most suggestive results were obtained with petioles of *Phaseolus multiflorus*, which were held firm at two distal zones about 1 cm. apart by being tied between pairs of sticks (1945, p. 77, and Figs. 9, 10). It was found that in the part between the fixed zones the prominent dorsal ridges curved upwards quite strongly, and this was favourable to Rawitscher's hypothesis: for on that hypothesis the dorsal half of a strophic organ, such as a petiole, has properties like those of a shoot in respect of its growth in the transverse direction, while the ventral half has properties like those of a root. So it agrees with this hypothesis that the dorsal ridges curved upwards as if by a negative geotropism working in the transverse direction. Correspondingly a ventral ridge should curve downwards on this hypothesis, but petioles with prominent ventral ridges are not easy to find, if they exist at all. Fairly common, however, are petioles which are just wedge-shaped ventrally, so that their morphologically mid-ventral lines can be recognized in transverse sections, and amongst these are the petioles of *Scrophularia verna* and *Sambucus nigra*, which respond very well, and also those of many *Umbelliferae*. In such

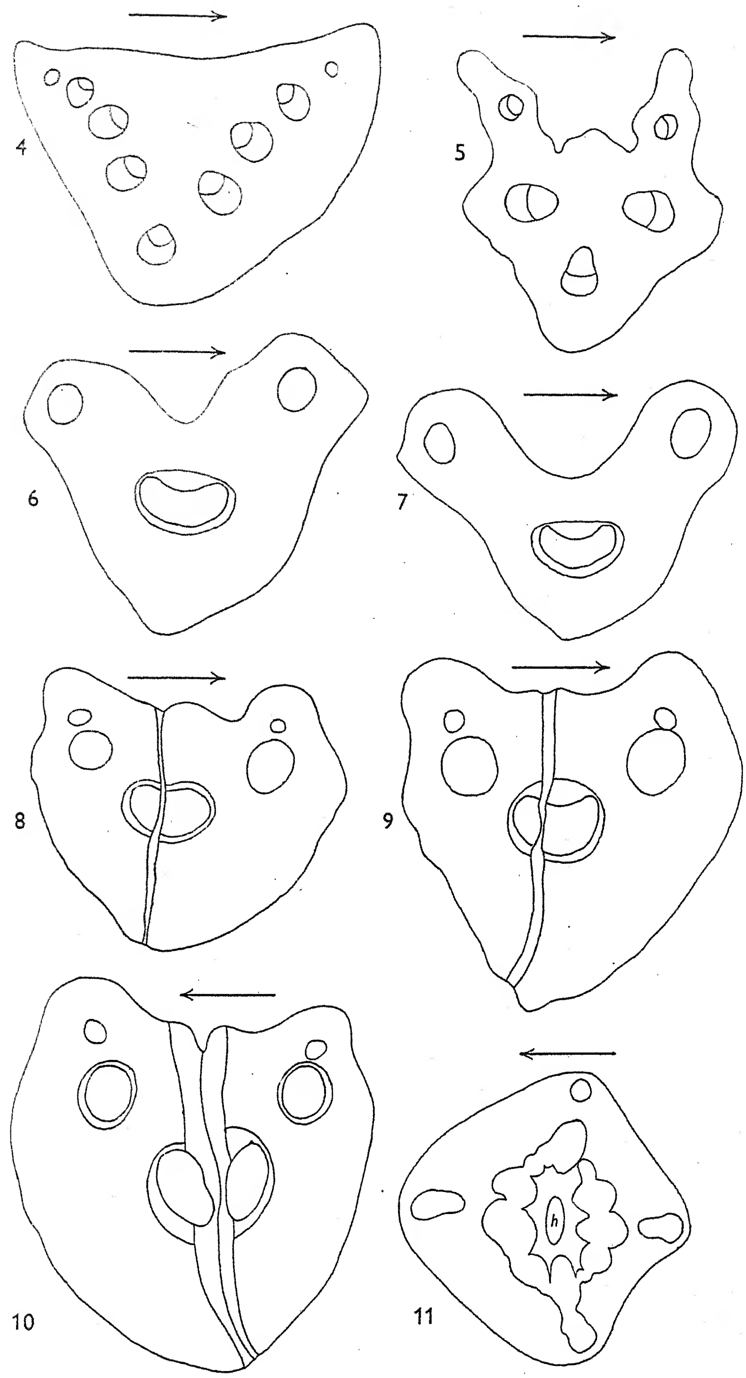
petioles stimulated similarly in constraint the mid-ventral lines might well be displaced downwards on Rawitscher's hypothesis, and accordingly some similar experiments were made on them.

The petioles of young leaves of these kinds of about half the final length were fixed in plasticine between sticks at two zones near their distal ends from 0·5 to 1·0 cm. apart, and the pots containing the plants were then placed horizontal in overhead light so that the fixed leaves were horizontal and on edge. The leaves were left to be stimulated by gravity and light for periods of from 7 to 10 days, and the parts of the petioles between the fixed zones, which were too short to twist more than slightly, were then pickled and examined in transverse sections. Figs. 4–7 show transverse sections through these regions of one petiole of *Aegopodium podagraria*, one of *Sambucus nigra* and two of *Scrophularia verna*. The arrows show the directions of gravity and overhead light during the stimulations. It can be seen that in all these petioles the morphologically mid-ventral line has shifted towards the side which was *uppermost* during stimulation, which is contrary to what would be expected on Rawitscher's hypothesis. Three other petioles of *Scrophularia verna* showed similar shifts. The morphologically dorsal halves have not shifted much, but in *Sambucus* (Fig. 5) and in one petiole of *Scrophularia* (Fig. 6) one of the dorsal ridges or corners has curved upwards slightly.

A different method was used for the petioles of *Lunaria biennis* which have no obvious mid-ventral line. It was found that a short glass needle, only 60 or 70μ in diameter, pulled out from a rod, could be passed transversely through the distal part of a petiole with confidence that it did not bend appreciably: and it was found that a needle so thin as this usually caused hardly any regeneration, if withdrawn again after being passed through, but yet left a narrow visible trace, so that the original dorsiventral plane of the leaf was marked. Accordingly the petioles of three young leaves of *Lunaria*, of about the usual size, were pricked through in this way within a short distal region intervening between two zones that were fixed in plasticine between sticks, as in the last experiment. The pots containing the plants were placed horizontal so that the leaves were stimulated on edge for periods of from 5 to 10 days, and then the petioles were pickled and sectioned transversely.

Figs. 8–10 show the sections through the traces left by the pricks. It can be seen that in all three petioles the parts of those traces within the ventral halves have curved or shifted distinctly towards the side that was uppermost during the stimulation, in agreement with the results of the last experiment. In two of these petioles, shown in Figs. 8 and 9, there was practically no regeneration and within their parenchymatous parts the tissue visibly affected by the prick was only two cells wide. But in the third petiole, shown in Fig. 10, there was considerable regeneration.

These results may seem inconsistent with those of the experiments reported previously (1942, p. 17; 1945, p. 76), in which petioles of various species including *Lunaria biennis*, and also incidentally pulvini of *Phaseolus*, were stimulated on edge while fixed with a rather different method to prevent them from twisting as wholes. For it was there stated that the cortex appeared to have shifted or twisted round a little in the normal or positive direction relatively to the stele: and in twisting round in this direction the dorsal cortex would have shifted upwards relatively to the stele, but the ventral cortex downwards. However, from the drawings (1942, figs. 4, 5; 1945, figs. 5–8) it can be seen that this appearance of a twisting round of the cortex was due to changes in the dorsal halves only,



Figs. 4–10. Sections of various petioles stimulated on edge in constraint for many days, and Fig. 11, a section of a stem of *Pisum* similarly stimulated with the plane of the leaves horizontal. The arrows show the directions of the stimulus of gravity.
Fig. 4. *Aegopodium podagraria*, ×13.
Fig. 5. *Sambucus nigra*, ×13.
Figs. 6, 7. *Scrophularia verna*, ×13 and ×9·5.
Figs. 8–10. *Lunaria biennis* pricked through with a glass needle, ×13.
Fig. 11. *Pisum sativum* stem, with the central hollow marked '*h*', ×17.

the fairly flat dorsal surfaces of the petioles or pulvini being no longer parallel to the dorsal surfaces of the steles, and consequently the changes observed indicated only that the dorsal cortex had shifted or curved relatively to the stele towards the side that was uppermost during the stimulation. An exception to this indeed was the petiole of *Viola odorata* (1945, fig. 8), but in that petiole the apparent shift was very small and perhaps not genuine. In the ventral halves of these petioles and pulvini the outlines of the petioles and pulvini and of their steles are so curved that shifts of the cortex could not easily be detected in this way, and the cortex has no obvious mid-ventral line that would reveal a movement of the ventral half as it does in other species. So it is quite possible that in the previous experiments also the ventral cortex really shifted towards the upper side. Those experiments should be interpreted as revealing only the shifts in the dorsal halves, and they therefore do not indicate, as they at first seemed to do (1945, p. 77), that it is the cortex which develops the twisting force.

Since the present experiments showed that the ventral cortex, as well as the dorsal, shifted or curved upwards in petioles fixed on edge, as if by a negative geotropism working in the transverse direction, it seemed of interest to find out whether it is only in dorsiventral and strophic organs, such as petioles, that the cortex shifts in this way, or whether it may do so in orthotropic stems also. So for this purpose two pots, each containing a young pea seedling (*Pisum sativum*), were placed horizontal so that the plane of the leaves, which are in two opposite rows, was also horizontal. This is a plane of bilateral symmetry of the shoot, and it is marked externally by two opposite corners of the four-cornered stem. The stem was fixed at two zones, about 6 mm. apart, near the top of a young internode of about half the final length, and was left for 7 days to be stimulated by gravity, and then the part between the fixed zones was pickled and examined in transverse sections. Fig. 11 shows that in the stem illustrated the two corners of the cortex which marked the plane of the leaves and were on the flanks during the stimulation have curved or shifted slightly towards the side that was uppermost, as if by a negative geotropism working in the transverse direction. In the other stem the appearance was similar. So the upward curve or shift of the parts of the cortex which are on the flanks during prolonged stimulation can take place in orthotropic stems also, and may perhaps have nothing to do with the strophic responses of dorsiventral organs such as petioles. But this of course does not alter the conclusion that the upward curve or shift of the ventral cortex in petioles stimulated transversely is unfavourable to Rawitscher's hypothesis. For on that hypothesis the ventral half of a strophic organ is positively geotropic in the transverse direction and should therefore curve downwards if at all.

Yet the positive torsions of the distally fixed petioles and rachises of detached leaves show in the writer's opinion, for reasons given previously (1942, p. 3; see also 1945, p. 80), that the strophic responses of these organs do depend on changes of some kind in the distribution of growth in the transverse direction, and consequently if these changes are not exactly of the kind which Rawitscher proposes, the question remains of what kind they are. This question might perhaps be studied in connexion with the torsions discussed previously (1945, p. 77), which are caused by applying auxin to these organs on one flank.

SUMMARY

1. Previously the writer used two methods for determining the direction of geostrophic torsion in leaves fixed distally and stimulated on edge. In the first method (1942) the

leaves were cut off completely, and in the second (1945) they were left attached at the base by a thin flexible conducting strand.

2. Further experiments have shown that the second method is faulty, since it sometimes leads to torsions which are not geostrophic, but due to other causes. So the results obtained with it must be rejected.

3. In distally fixed petioles of the simple leaves of *Lunaria biennis*, *Scrophularia verna* and *Nepeta hederacea*, when these leaves are detached and stimulated on edge, the direction of geostrophic torsion is normal or positive, as previously (1942) it was shown to be in pinnate leaves of several species. So the direction is positive in all petioles and rachises so far tested, and negative in certain pulvini only (1942, 1945).

4. When petioles of various species are prevented from twisting as wholes and stimulated on edge for many days, the ventral cortex, like the dorsal cortex, curves or shifts towards the upper side. This movement of the ventral cortex is opposite to that which would be expected from the particular form of transverse growth hypothesis suggested by Rawitscher (1932) for explaining the torsions.

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THE ECOTYPE CONCEPT

A CONSIDERATION WITH APPRECIATION AND CRITICISM, ESPECIALLY OF RECENT TRENDS

By W. B. TURRILL

In two papers, published in 1922, Turesson (1922*a*, *b*) introduced the ecotype concept and its importance in the study of the constitution and origin of species was almost immediately recognized. Ecologists and taxonomists alike appreciate the value of combined field observations and controlled cultural experiments. There was some criticism, in part justified, that the field studies of populations and of the conditions of their environment were insufficiently extensive and intensive and that the ecotype concept was based too much on selected individuals and not on the study of whole populations or of sufficiently large random samples of such. Nevertheless, Turesson's researches have opened up new lines of research and full recognition of his great contributions to the study of species problems must be gratefully accorded by anyone familiar with the facts.

There is no intention, or need, to give details of the early investigations on ecotypes. A very useful summary is given by Barton-Wright (1932). More recently, Gregor (1944) has published a most valuable summary of much recent research and trends of thought in this subject. The present paper is concerned mainly with two matters: the full significance of changes in definition of terms first used by Turesson in 1922, and the relation between genecology and taxonomy. Gregor (1944) touched on both these problems which were also referred to by the writer in an earlier paper (Turrill, 1938) and more recently in a review (Turrill, 1942). An investigator is unavoidably impressed more by his own experiences, by the examples with which he himself has worked, and by the difficulties he meets, than by those of others, and the value of concepts, terms, definitions, and schemes of classification can only be tested pragmatically. Genecologists have often criticized taxonomists, sometimes not without reason, but sometimes from a misconception of the taxonomist's functions. Taxonomists have too often ignored these criticisms and indeed the whole experimental work of genecologists, though there is increasing improvement in this respect. The present writer again expresses his appreciation of both the methods used and the results obtained in genecological research and is confident that any criticisms he makes will be accepted in the constructive spirit in which they are offered.

Terms and their definitions

From the accounts published in his two 1922 papers it is concluded that Turesson at first based his terms and their definitions on observations and experiments, at least mainly, on Swedish plants of some twenty species belonging to thirteen genera of various families (Gramineae, Chenopodiaceae, Caryophyllaceae, Crassulaceae, Primulaceae, Plumbaginaceae, Solanaceae, Dipsacaceae, and Compositae). On the basis of these studies the three important terms coenospecies (cenospecies in American spelling), ecospecies, and ecotype were proposed. In considering these, and other terms, it is essential to give actual

quotations, since some of the difficulties which must be faced are connected with subtle differences in definitions, which, until their significance is emphasized by reference to examples may appear to be mere quibbles.

The first term used by Turesson (1922 *a*, p. 102) is *ecospecies*, but this is not immediately defined. In the same paper (p. 112) we read: 'The term *ecotype* is proposed here as [an] ecological unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat. The *ecotypes* are then the ecological sub-units of the ecospecies, while the *genotypes* are purely Mendelian sub-units of the genospecies.' In the second, longer, paper of the same year (1922 *b*) we find (pp. 244, 245) the following: 'The term *ecospecies* has been proposed (Turesson, 1922) to cover the Linnean species or genotype compounds as they are realized in nature.'

'It is evident that we do not find realized in nature the whole possible range of combinations within such an ecospecies because of the control of living and non-living factors of the outer world....'

'It seems appropriate—for theoretical reasons—to denote the total sum of possible combinations in a genotype compound by the term *coenospecies*.'

'The term *ecotype* seems to be an adequate expression, and is therefore proposed for the ecological unit, to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat.'

There is no doubt from the context that Turesson was regarding species problems from the ecological standpoint when he proposed the above terms. Thus he notes that the purely genetical side of 'the species problem' (the present writer prefers to use the plural) is fairly well understood, but that we have nothing like a reliable picture of the significance of ecological factors in the differentiation process of organisms. He aims at 'an understanding of the Linnean species from an ecological point of view'. It is perhaps better to replace 'Linnean' in such expressions by 'generally accepted taxonomic'. Turesson was, therefore, justified in his use of the prefix *eco-*, since both ecotype and ecospecies are so far regarded by him as ecologically delimited. That he did not, in 1922, directly include genetical criteria in his 'eco-' concepts seems to be indicated by the contrasted diagrams published in the second paper (1922 *b*, pp. 344–5). Further, the coenospecies is conceived as a theoretical unit, as the expansion of an ecospecies to its utmost limit with all the theoretically possible gene combinations in a 'genotype compound'. It is, of course, probable that all the deductions which could be drawn from these first concepts were not immediately realized, but the experimental data given, the form in which they are given, and the lucid discussion of the results obtained indicate that the intention was to keep the ecological and genetical viewpoints distinct and that it was the usually accepted taxonomic species which was thus to be regarded. A paper published the next year (Turesson, 1923) contains sentences supporting this conclusion. 'The Linnean species represents as such a much [most] important ecological unit, to which unit the name *ecospecies* has been given by the present writer.' 'The term *ecotype* has been proposed by the writer to cover the ecological sub-unit of the ecospecies arising as a result of the differentiation of the species-population in response to particular habitat conditions.'

In a later paper, Turesson (1926) shows that he is making the ecotype concept more extensive in that he includes other European examples, in addition to Scandinavian. He distinguishes modifications, ecotype formation, geographical isolation, and isolation through apogamy. Of particular interest in this paper is his recognition of Alpine

ecotypes, all of which he suggests should be named, under the species, *Oecotypus alpinus*. Extending this nomenclatural scheme he suggests *Oect. arenarius*, *Oect. campestris*, *Oect. salinus*, etc. He notes, however, that the high mountain (alpine) races of a species in the Alps and corresponding races of the same species in the Scandinavian highlands are not the same but nearly always show small differences. One other matter is partially clarified in this paper since Turesson refers to ecotypes as being groups of nearly related biotypes that have become differentiated in a certain habitat out of the heterogeneous species population through the sorting and controlling action of the predominant ecological factors of the habitat. A widely spread species can differentiate out a large number of ecotypes for many different habitats. Apparently this means that in addition to the differentiated ecotypes there remains a heterogeneous species population not limited to any precisely determined ('particular') habitat. This is in agreement with the diagram (1922 *b*, p. 344) already mentioned though in a corresponding respect the contrasting diagram for a genospecies (p. 345) is inaccurate or incomplete since every individual in a genospecies (or any other unit of biological classification) must belong to some genotype.

Turesson's earlier experimental research was concentrated on ecotypes within the limits of generally accepted species and his early conceptions of ecospecies and coenospecies had much less experimental backing. This may account for a decided change in definitions. We quote (Turesson, 1929, from the summary) definitions distinguishing three kinds of species:

'(*a*) *Ecospecies*: An amphimict-population the constituents of which in nature produce vital and fertile descendants with each other giving rise to less vital or more or less sterile descendants in nature, however, when crossed with constituents of any other population. (Illustrated by *Geum rivale*, *Salix viminalis*, *Viola arvensis*, etc.)

'(*b*) *Agamospecies*: An apomict-population the constituents of which, for morphological, cytological or other reasons, are to be considered as having common origin. (Illustrated by *Alchemilla vulgaris*, *Antennaria alpina*, etc.)

'(*c*) *Coenospecies*: A population-complex the constituents of which group themselves in nature in species units of lower magnitude on account of vitality and sterility limits having all, however, a common origin so far as morphological, cytological or experimental facts indicate such an origin. (Illustrated by *Capsella bursa pastoris*, *Erophila verna*, etc.).'

The agamospecies may be a useful concept but it would appear to belong to a different category from ecospecies and coenospecies. Difficulties must surely arise when 'morphological, cytological or experimental facts' show that apomicts are more closely related (taxonomically and phylogenetically) to certain amphimicts than to one another. When, in other words, both amphimicts and apomicts are most reasonably classified together it seems artificial and for a majority of purposes scientifically inconvenient to separate and group together the apomicts as an agamospecies. In some genera there probably are, at least within limited geographical areas, what are most conveniently termed agamospecies, but the concept of agamospecies by no means solves the difficulties of classifying apomicts.

With regard to ecospecies and coenospecies we now have the fertility-sterility criterion definitely introduced but this is basically a genetical and not an ecological criterion. It is, of course, none the worse for that, but the term *ecospecies* becomes misleading. However, in 1929, the fertility-sterility criterion is not made absolute. Two plants belong to different ecospecies if on crossing with each other they give 'rise to less vital or more or less sterile descendants in nature'. It is what happens 'in nature', not in the experimental ground,

that matters. 'More or less sterile' is very vague and it is not entirely clear just what 'vital' includes even after a careful reading of the whole paper, though in the example of *Salix caprea* × *S. viminalis* it is noted that reduced vitality of individuals in the F_2 generation is shown by 'abnorme Periodizität, herabgesetzte Winterfestigkeit, verringerte Widerstandskraft gegen parasitische Pilze usw.'. Such reduced vitality obviously depends in part on environmental conditions and individual factors in it might under other ecological conditions, than those of Sweden be at least neutral to the action of natural selection, if not advantageous. Stress is laid on the fact that ecospecies (and, of course, coenospecies) do not, in nature, hybridize together to the extent that they form hybrid populations ('hybrid swarms'). What is not stated is that even this criterion is not absolute. For example, *Geum rivale* and *G. urbanum* are quoted (Turesson, 1929, p. 329) as a pair of species which can be artificially crossed together but of which only single hybrid individuals occur in nature. However, it has been clearly shown (Marsden-Jones, 1930) that a hybrid population can occur in nature and the writer can confirm from personal observation the hybrid swarm nature of the Bradfield, Berkshire, population. Yet *G. urbanum* and *G. rivale* do, over by far the greater part of their ranges, remain distinct as clear-cut morphological and ecological entities. What is still needed is a detailed study to determine exactly the physiological factors upon which selection acts to limit them to different habitats. Till these are known the genecology can only be stated in very general terms.

It has been necessary to occupy a considerable amount of space in analysing Turesson's concepts. This is some measure of their importance. In his later papers, over a dozen of which are available, Turesson generally seems to avoid clearly classifying and naming the genecological units he investigated and to be content with giving the valuable experimental data which help so much towards the understanding of the make-up of taxonomic species. The genecological method does seem to enable the student 'to get inside the species', to study it from within, and, in combination with field-studies, to understand it as a living, and therefore changing, population.

We turn now to consider the use made by other genecologists of Turesson's concepts, and the modifications they have made. Two quotations from Gregor's papers are given, the first (from a joint paper) because it fairly sums up Turesson's later standpoint and the second because it shows clearly a more recent trend. Gregor, Davey and Lang (1936) say: 'The present writers interpret Turesson's classificatory units as follows:

'*Coenospecies*. A group distinguished by morphological, physiological or cytological characters, or a combination of these; separated from all other plants by sterility or by failure of hybrids to produce viable seed. Parts of a coenospecies may have become separated by natural barriers, e.g. oceans or mountain ranges, so that all potential hybridizations cannot occur in Nature.

'*Ecospecies*. A group also distinguished by morphological, physiological or cytological characters, or a combination thereof; separated from other parts of its coenospecies by restricted interfertility or by failure of hybrids to establish themselves in Nature.

'*Ecotype*. A population distinguished by morphological and physiological characters, most frequently of a quantitative nature; interfertile with other ecotypes of the ecospecies, but prevented from freely exchanging genes by ecological barriers. Spatially widely separated ecotypes may exhibit characters determined by genes restricted to the geographical regions in which they occur.'

The following points must be noted with regard to these definitions. The coenospecies has become a concrete 'group', an existing population and not a theoretical extension of an ecospecies. A coenospecies and an ecospecies are distinguished by the former being sterile when crossed with another coenospecies or by the F_1 between them being completely sterile, while the latter shows 'restricted interfertility' when crossed with another ecospecies *or* hybrids between them fail 'to establish themselves in Nature'. There is thus a double criterion for ecospecies and the question must arise (see below for *Silene*) which is to be given preference. The differences between an ecospecies and an ecotype are not clearly contrasted. Ecotypes are interfertile one with another (as shown presumably by controlled experiments in the experimental ground), but the '*or*' in the definition of ecospecies leaves it open whether the same may not be sometimes true for ecospecies. Nothing is said about hybrid populations and it is not clear whether failure of establishment of hybrids means that individual hybrid plants cannot establish themselves as seedlings and/or grow to maturity or whether hybrid swarms cannot become established. Later (Gregor, 1939), we find shorter definitions, as follows: 'The use of the following "specific" terms is advocated: *Coenospecies*, a population which is incapable of exchanging genes with other populations, even when given the opportunity. *Ecospecies*, a population with an inherently low capacity for exchanging genes with other populations of its coenospecies.' Other terms are also introduced, including: '*Cline*,* any gradation in measurable characters' and '*Ecocline*, a cline apparently correlated with an observable ecological gradient.' *Ecotype* is now defined as 'a particular range on an ecocline'. It follows that of the three genecological terms with which we started only *ecotype* remains under this designation, for coenospecies and ecospecies are defined in purely genetical or cytogenetical terms. 'Inherently' in this connexion must mean having nothing to do with environmental conditions.

The experimental researches mainly on American genera and species, initiated by Clements & Hall and extended by Clausen, Keck & Hiesey have rightly attracted a great deal of attention. The value of this work to taxonomic theory and practice must be fully acknowledged but we are concerned here only with one aspect of it—the definition and application of terms. For this purpose we may consider two recent publications (Clausen *et al.* 1939, 1940). Clausen *et al.* (1939) use the three terms *cenospecies*, *ecospecies* and *ecotype*. The *ecotype* is distinguished by the absence of genetic isolation; the *ecospecies* shows partly genetic and partly ecologic isolation; the cenospecies has absolute genetic isolation. The stress is obviously on sterility or fertility between such groupings as occur in nature and most extensive, fully controlled, crossing experiments must be made to determine the status of any such group. For ecospecies of one cenospecies, it is stated that 'if crossed, their hybrids are partially sterile, whereby non-viable sex cells are eliminated, or the second generation of offspring is weak; most often both these conditions obtain. Weakness of the second generation may manifest itself in various ways: many individuals are slow-growing dwarfs, or subnormals, others are very susceptible to diseases to which the grandparents and even F_1 are immune; others again may be structural or anatomical misfits, to mention some examples....A small percentage of the total offspring may be vigorous and fertile but tends to be eventually absorbed into one or other of the parental species.' In 1940 a 'glossary of important terms' was printed (p. vii)

* *Cline* is a term, proposed by Huxley, which is not further commented upon here.

but only the comments under *ecospecies* need be noted here. An ecospecies is a group of plants 'within the cenospecies whose members are able to interchange their genes without detriment to the offspring. Ecospecies are separated from one another by internal barriers that prevent such free interchange'.

In the application of their concepts to the taxonomic arrangement of the groups as recorded in their 1940 publication Clausen *et al.* generally equate the ecospecies with the taxonomic species and the ecotype with the taxonomic subspecies. There are, however, exceptions. For example, *Potentilla glandulosa* ssp. *nevadensis* is said to consist of two ecotypes, but 'since the differences between the two are not sufficiently distinct to be recognized in the field or in the herbarium with certainty, the two ecotypes are here included in one subspecies'. The experimental breeding evidence, so far as reported, supports the classification if the basis of this be accepted, but it appears to be meagre. For *Potentilla glandulosa* and its allies, three species are accepted and within *P. glandulosa* eleven subspecies (thirteen ecotypes), but the only crossings recorded are subsp. *typica* × subsp. *reflexa*, subsp. *typica* × alpine ecotype of subsp. *nevadensis*, and subsp. *reflexa* × alpine ecotype of subsp. *nevadensis*. Thus the determination of ecotype groups as such is based mainly on field and cultural studies (both of which seem to have been extensive and intensive) but not on controlled breeding. For a full test of the fertility of the thirteen ecotypes of *P. glandulosa* with one another every one should be crossed with every other and this should be done reciprocally. Instead of 156 crossings only three are recorded. The experimental crossing in *Zauschneria* was more extensive and between a smaller number of accepted units. The work on the *Achillea millefolium* complex must interest British botanists, but only one controlled crossing is recorded and the recognition of ecotypes as such and not as ecospecies is apparently based almost entirely on cultural not hybridization experiments. These comments, of course, are not criticisms of the methods used and the results obtained, so far as they go, but they do show the enormous amount of controlled breeding work that must be done, and correlated with field and cultural experiments, before any group can be satisfactorily established on the basis of the definitions accepted, if these are rightly interpreted by the writer. With very slight modifications the same remarks would apply to Winge's work on *Erophila* (Winge, 1940). Lawrence (1945), in *Deschampsia caespitosa*, recognizes a number of ecotypes as a result of cultural experiments and field observations, but experiments for fertility or sterility between the groups accepted are not recorded, and apparently have not been made. There is no direct evidence that some of the supposed 'ecotypes' are not in some degree 'ecospecies'. The value of the facts experimentally determined and of their correlation with field observations is fully recognized by the present writer, particularly the emphasis upon physiological characters, but the absence of genetical facts obtained by controlled breeding makes the proposed ecotypical scheme tentative if the more recent definitions of genecological terms be accepted.

Genecology and taxonomy

In the above account of the definitions and applications of the three main genecological terms reference has been made only to the works of Turesson and a few subsequent authors. One may fairly say, however, that there has been an increasing tendency in theory to emphasize sterility-fertility criteria at the expense of geographical-ecological

and in the practice of our American colleagues to consider that taxonomic research ends with the regional ecotype. There is no doubt that the majority of the ecotypes early accepted as such by Turesson are taxonomically small groupings (micro-paramorphs) while the ecotypes (mostly equated with subspecies) of Clausen *et al.* are, with some exceptions, of a higher taxonomic status. One cannot help thinking that within regional ecotypes there may be other, smaller, ecologically delimited groupings which would equally well conform to the definition of ecotype. There would thus be ecotypes within ecotypes. Indeed, Kovalev (1939) has introduced the term subecotype. Apart from this difficulty the taxonomist cannot help objecting to the overwhelming importance that is given to sterility-fertility criteria at the ecospecies level. In spite of attempts to introduce 'lowered vitality' criteria ecospecies as such are distinguished, in theory at least, from ecotypes by inherent intersterility. 'Sterility' is a very wide term and tests for sterility or fertility can never be exhaustive. Further experiments with newly obtained stocks or under different conditions may result in upsetting previous conclusions. This, however, need not be overstressed for something similar is a limitation of all inductive methods. To the taxonomist it is the artificiality of the classification that often results from using one criterion that makes him hesitate to make his 'species' necessarily and always conform to the genecologist's ecospecies. The taxonomist accepts the most difficult task of balancing morphological, ecological, and genetical data, using the three words in the widest possible senses, before he delimits his units. This, of course, is his ideal, rarely attained because an alpha taxonomy has usually to be provided before ecological and genetical data are available. Genecological research, more than anything else, must help towards attainment of the ideal omega taxonomy, but unless genecological classification, as hitherto proposed, is accepted as a special classification not necessarily coinciding with a final general classification it may to some extent delay progress.

The orthodox taxonomist may have his own aims and methods. He may claim taxonomy is a subject in its own right and wish to warn off intruders. His tradition and system of nomenclature may date from Linnaeus and he may be more or less contented with it. That one system of classification and nomenclature has to serve for phanerogams, cryptogams, bacteria, viruses, and fossil plants (and a very similar system for extant and extinct animals of all groups) may make it impossible to use the same terms always with exactly the same shade of meaning. It remains a fact that every 'character' and every variant has some importance to the taxonomist since he has to serve not only the ecologist but also the cytogeneticist, anatomist, physiologist, phylogenist, evolutionist, and the applied botanist. His classification must be 'general'. He must consider all available data and balance up accordingly. He can only do this because there is naturally much correlation between different criteria and often a classification on morphological data agrees with one on ecological or genetical data to a high degree. There are, however, examples known of breakdown in such a correlation and then there may be special advocacy for greater classificatory value to be given to one or other set of criteria. The taxonomist will only fulfil his function properly if he remembers the wide use that may be made of his classification and without bias determines the taxonomic status of his groups from consideration of all the correlations that remain.

The taxonomist of wide experience wonders if those botanists who postulate inherent sterility as the essential criterion of specific distinction realize fully what this would involve if uniformly adopted throughout plant groups. Every other criterion would go

by the board. A great many 'species' would become enormously large, in the taxonomic sense, and for all purposes other than those depending solely on sterility-fertility criteria a cumbrous nomenclatural system would have to be devised. It can be well argued that a modification of the pre-Linnean nomenclatural system has, for certain purposes, advantages over the binomial system but its unwieldy nature is at present against its general acceptance. Fertility and sterility are of all degrees and with many 'causes'. The distinction between inherent sterility and the absence or rarity of natural crossing due to external causes is made, so far as the resulting differentiation of groups is concerned, by the botanist and not by natural selection. Sterility may result from changes in chromosome number, from alterations in chromosome structure (inversions, etc.), or from gene mutations.

Once isolation is established between groups, differences between the groups tend to accumulate but there seems no *a priori* reason against the occurrence of genetical or cytogenetical changes which result in inter-group fertility where there was previously intergroup sterility. The main argument used in favour of the high value given to inherent sterility barriers as compared with environmental barriers is that the latter are easily changed or a plant group can easily migrate to another environment while 'the leopard cannot change his spots'. The general taxonomist, who has to deal with the results of evolution, can usually be trusted to keep a fair balance in any dispute between 'nature and nurture'. This has been, and is, rightly or wrongly, the working standpoint of the plant taxonomist: that groups that are kept recognizably distinct in nature must be treated on their merits whatever the barriers, cytogenetical, ecological, or geographical, keeping them from merging into one larger group. What would the genecologists do with the parents of the hybrid orchid genera *Potinara* and *Burrageara* each of which has been built up artificially from four different species belonging to four different genera (*Orchid Hybrids*: Sander's List, 1931)?

Nevertheless, the writer, in common with many other taxonomists, is in very wide agreement with the genecologist's standpoint, and especially with the original viewpoint of Turesson and with the extended methods of later workers. The necessity for experiment, the need for wide field studies, the distinction between modifications and inherently determined differences, the realization of the meagre factual basis for general phylogenetic schemes, recognition of the species as the most important working unit of the taxonomist, and so on, are not only accepted and welcomed but agree with conclusions reached independently.

Genecological methods are contributing much, and will contribute more, to the solution of taxonomic problems. The writer and his colleague, E. M. Marsden-Jones, can claim to have proof of this for the British flora from their own researches during the past 20 to 25 years. The one more or less serious point at issue between genecologists and the average orthodox taxonomist is whether or not genetical barriers shall be given predominance over ecological and distributional barriers in evaluating groups for purposes of classification. Possibly further research will show that the number of groups in dispute is small in practice—that correlation between genetical and ecological barriers is the rule. One difficult example may be taken in illustration of present difference of opinion.

Marsden-Jones & Turrill (1928–40) have investigated genecologically and taxonomically the two taxonomic species *Silene maritima* and *S. cucubalus* (*S. vulgaris*). The results of studying British populations are mostly in print but extensive investigations

on continental material have not yet been published or fully worked up owing to the war.

S. maritima and *S. cucubalus* are kept as taxonomically distinct species for the following reasons, amongst others, considered together:

(1) They are distinguished by over a dozen morphological characters which show a high to very high correlation. There is no difficulty in determining individual plants.

(2) They are distinguished by a number of physiological characters additional to those obviously associated with morphological characters.

(3) They have different, though overlapping, geographical ranges.

(4) They have very distinct natural ecological tolerances.

(5) Populations of the two remain distinct. When they meet in nature, very few hybrids can be found, and gene exchange is decidedly limited. There is no tendency towards natural amalgamation of the two to form one more variable species or a hybrid swarm.

(6) There is circumstantial evidence that the two have been distinct since, at least, immediately preglacial times.

The reasons for reducing the two to subspecies (ecotype) status are:

(1) A single morphological character may break down, usually because of mutation, very rarely through gene infiltration, perhaps occasionally through retention of hidden recessive genes from a common ancestral stock.

(2) There is no inherent sterility between the two as tested by numerous reciprocal crosses made under full control in the experimental ground. Good F_1, F_2, and later generations and back-crosses are usually obtained without difficulty.

This is a brief but fair summary of the situation. If the genecological terminology be used on the basis of fertility-sterility, *S. maritima* and *S. cucubalus* are ecotypes of one ecospecies, or following the procedure of Clausen *et al.* they are two subspecies of one species to which the name *S. maritima* has to be applied on priority grounds. This is clear so far but then there comes a difficulty. Up to the present, within the British Isles, we have not been able to distinguish clear-cut populations morphologically and ecologically delimited within either *S. maritima* or *S. cucubalus*, i.e. to distinguish ecotypes within them, though three such populations of *S. maritima* (Portland end of Chesil Beach, Brecknock Beacons, and Skye) may eventually have to be considered as such. When, however, continental populations are considered, the situation is different. Turesson himself (Turesson, 1925, pp. 153–6) records ecotypes within *S. maritima*, though they appear to be very small paramorphs the like of which we could match amongst British plants but which do not in our flora, so far as observed, constitute ecologically distinct populations. Icelandic material, as studied in the field and in the experimental ground at Kew must be considered ecotypically distinct from British material. With regard to *S. cucubalus* the complications are much greater. Apart from *S. alpinus*, *S. glareosa*, and other mountain groups some (but probably not all) of which might be considered ecotypes relative to the many-flowered tall and erect growing lowland *S. cucubalus* s.s., which, however, also ascends in hay fields high up into the Alps, there are other ecotypic groupings which have been studied in and from southern and central Europe. In crosses between some continental stocks and some British stocks, within the range of plants with which we have worked, there is partial sterility, sometimes in F_1, sometimes in F_2. The results, however, are complicated and the data have not yet been completely analysed. There are also groups (as *S. thorei* from north-western France,

S. commutata from Sicily, and *S. reiseri* from the western Balkan Peninsula) which we have not yet been able to study experimentally. Any comprehensive scheme based on experiments cannot yet be formulated and it is most convenient to retain, as a working basis, the ordinary taxonomic conception of *S. maritima* and *S. cucubalus* as two species separated by ecological barriers, whether genecologically one recognizes them as ecotypes, as ecospecies, or as coming somewhere between the two.

To sum up, it is concluded that taxonomy has to have a wider basis than genecology, that while genecological research has much to contribute to taxonomy genecological classification, if strictly adhered to, is a special and not a general classification, and that it is highly desirable to attain and maintain stability in the concepts and terms used in genecology. The special genecological methods can be entirely absorbed into orthodox taxonomy, its classification sometimes coincides, or can be made by slight modifications to coincide, with the more general classification which is necessary if taxonomy is to fulfil its proper and extensive functions. Sometimes, however, the taxonomist has to give greater classificatory weight to the results of ecological and geographical barriers than does the genecologist. The taxonomist is concerned in classifying what he finds more than with the results obtained when natural barriers are artificially, and often very temporarily, eliminated. There are exceptions to this statement, as in the study and classification of cultispecies, and it in no way diminishes the importance, to the taxonomist himself, of experimental research.

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ON A PEAT FROM THE ISLAND OF BARRA, OUTER HEBRIDES

DATA FOR THE STUDY OF POST-GLACIAL HISTORY. X

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(With 2 figures in the text)

INTRODUCTION

During the Expeditions to the Hebrides led by Prof. J. W. Heslop Harrison a number of peats have been investigated. Their pollen statistics are being examined with a view to getting a picture of the post-glacial changes of vegetation to supplement that arrived at by a study of the present flora and fauna. Grateful thanks are here recorded to the King's College Research Committee for grants in support of this work.

For the Outer Islands there seem to be characteristic features for the peat profiles of individual islands, and it appears desirable to describe first one example, as near the average pattern as possible, so that the peculiarities of the others can be shown by comparison. For this purpose a profile has been chosen from a peat cutting taken near the pair of small fresh-water lochs, called Lochan nam Faoileann, situated about midway up the east coast of Barra.

The lochs lie at about 100 ft. O.D. and their contours, at least, may well be relatively new, since the water is quite shallow and at places peat beds are exposed at the edges. The peat cutting from which the samples were taken was some yards from open water and the peat was being removed right down to the rock. The depth was about 4 ft., but a little farther from the lake another cutting was observed to be some 6 ft. deep. Fraser (1943) reports large areas of similar peats from the Island of Lewis, in which 4 ft. was the most frequent depth. These shallow blanket peats are a widespread feature of the Outer Islands. Much deeper peats from the Island of Raasay (Inner Isles) show lake sediments, at least at the base, but, so far, such deposits have not been seen by the author on 'the Long Island', though both Lewis (1906) and Erdtman (1924) have found peats with underlying lake deposits on the Island of Lewis.

DESCRIPTION OF THE PEAT

The profile to be described shows a bottom layer of about an inch of dark brown peat full of bits of decomposed rock. Immediately over this is black buttery peat containing birch twigs and remains of *Phragmites*. Above is a rather indeterminate, much decomposed peat which gradually becomes more fibrous upwards with a more humified band around 50 cm. from the surface. This type of peat, though not studied in detail here, is generally produced from a mixed vegetation with *Scirpus caespitosus*, *Eriophorum vaginatum*, *Erica Tetralix* and *Calluna vulgaris* as the most conspicuous plants, and usually, as here, the amount of *Calluna* increases at the top.

Methods used

The samples taken from the cleaned cutting were collected in tubes in the ordinary way. Unfortunately, owing to inexperience of these Outer Island peats, only fifteen samples were taken; many more would have been desirable since accumulation proves to have been extraordinarily slow. For examination the peat was first digested with 10% aqueous KOH and subsequently treated, without drying, by Erdtman's chlorination-acetolysis technique (Erdtman, 1943). The lower layers were subsequently cleared of fine mineral particles with cold hydrofluoric acid. After washing, the sediments were mounted in fuchsin glycerine jelly.

Although small amounts of tree pollen were to be expected in these reputedly treeless islands, no difficulty was found in counting enough tree pollen on the slides so prepared, though the great preponderance of non-tree pollen (N.T.P.) made the work very laborious.

Distribution of spores and non-tree pollen

The quantities of spores and N.T.P. recorded for the different levels are shown in Fig. 1, calculated, in the usual manner, as a percentage of the total tree pollen in each sample. It will be noticed that the values are very high; for this reason the curves have been drawn at one-tenth of the horizontal scale used for tree pollen in Fig. 2. The total percentage of N.T.P. and spores is never less than 250% and approaches 4000% at the surface.

The two basal samples have high values of ericoid pollen, chiefly *Calluna*, and of *Sphagnum* spores, and are probably derived from a shallow turf. The large quantity of *Osmunda* there is a feature of considerable interest, but its stratigraphical importance should not be overemphasized, as the plant grows in quantity to this day on a lake islet nearby.

The *Phragmites-Betula* layer suggests at least a change in drainage and may possibly be related to the beginning of the lake in the area. The diagram shows a sudden fall in ericoid pollen and *Sphagnum* spores with an abrupt rise in grass pollen, which is exactly what might have been predicted.

In the fibrous peat, at depths of 80 and 60 cm. respectively, are *Sphagnum* maxima coincident with peaks in the curve for ericoids. In the layer of highly humified peat at 50 cm. the N.T.P. values are all relatively low, and a change in conditions is indicated above it by a temporary rise in the curves for grass and sedge accompanying a rise in ericoids. The extremely high values for ericoids in the uppermost layers are probably due to a local development of Callunetum. The vegetation growing on the top of the peat was extremely sparse, but what there was of it was almost entirely *Calluna*. By more careful analysis the *Potentilla* curve could probably be resolved into two components: the lower peaks in the *Betula-Phragmites* zone representing *P. palustris* and the upper *P. erecta*, an extremely common plant on the surface of the blanket peats to-day.

Ferns, other than *Osmunda*, have not been graphed, but they reach high values in the reed zone: *Pteridium* is 300% at 105 cm. and the unidentifiable spore intines of other ferns attain 250% at the same level.

The pollen of characteristic plants, even when present in quite small quantities, may often give a clue to the type of vegetation producing the different layers of peat. The

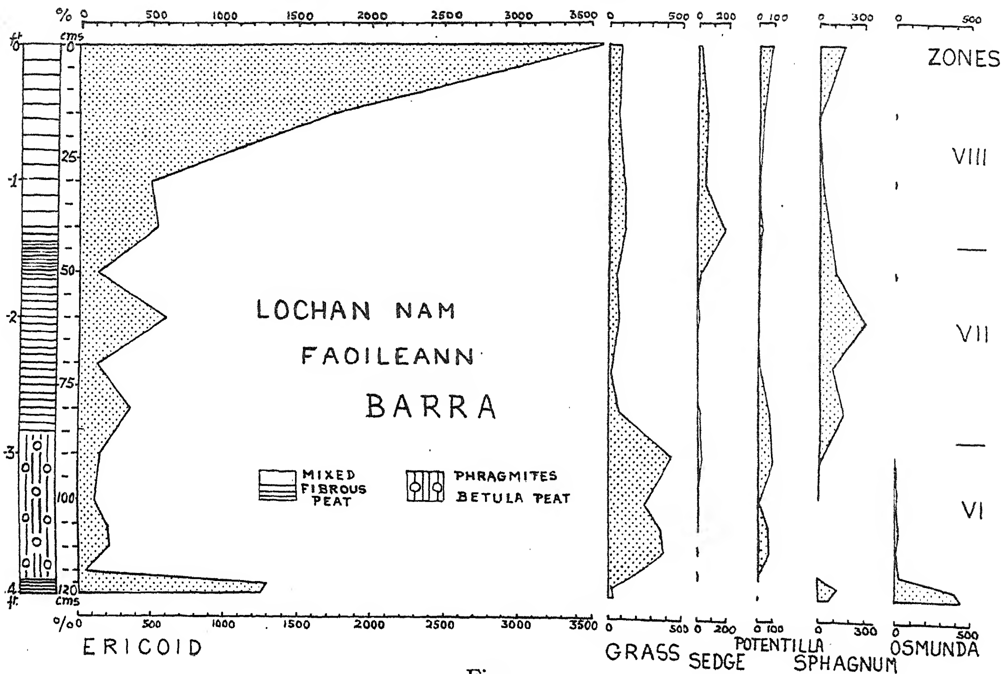
LOCHAN NAM
FAOILEANN
BARRA
MIXED FIBROUS PEAT
PHRAGMITES BETULA PEAT
ZONES
VIII
VII
VI
ERICOID
GRASS
SEDGE
POTENTILLA
SPHAGNUM
OSMUNDA

Fig. 1.

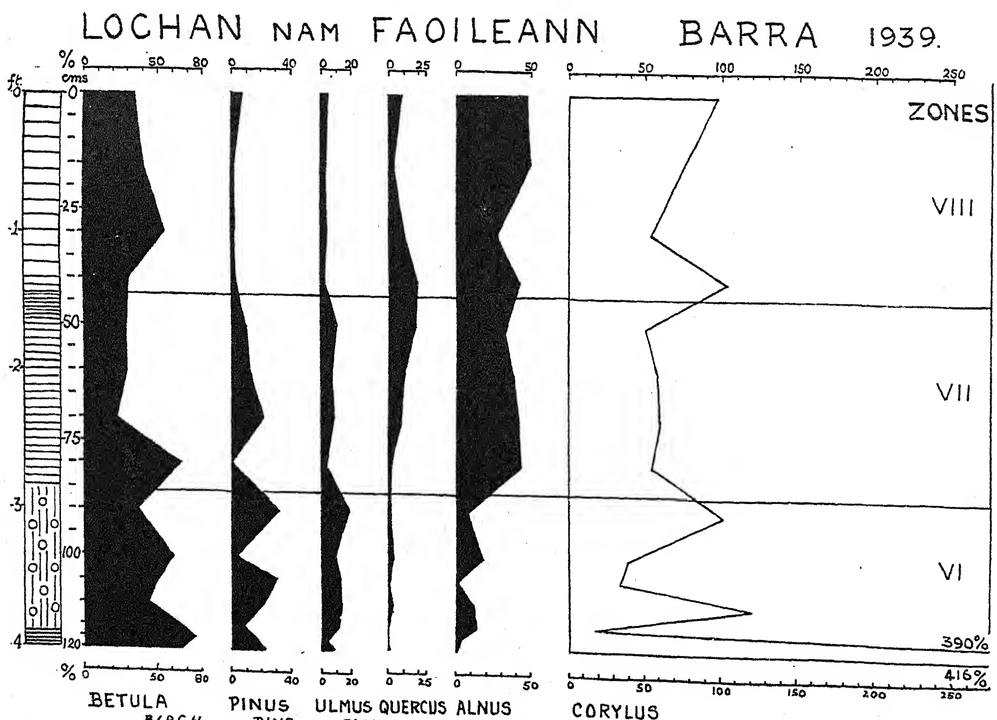
LOCHAN NAM FAOILEANN BARRA 1939.
ZONES
VIII
VII
VI
390%
416%
BETULA
BIRCH
PINUS
PINE
ULMUS
ELM
QUERCUS
OAK
ALNUS
ALDER
CORYLUS
HAZEL

Fig. 2.

upper layers here, for instance, contain pollen of *Polygala* and *Drosera*, whereas the reed zone carries *Menyanthes*. *Anthoceros*, however, seems rather a curiosity in the reed layers, and indeed there seems to be no record of the genus in the living state from V.C. 110.

Forest trees and hazel

The curves for tree pollen and hazel are drawn in Fig. 2, the hazel calculated separately as a percentage of the total for forest trees.

Perhaps the most noticeable feature of this diagram is the consistently high value for hazel, with an initial maximum of over 400%. This and the generally high birch values indicate that these two trees formed the main woody vegetation of the island. At different times other trees appeared in response to varying conditions: in the early part of the diagram pine and elm are important and later alder and oak. Lime is absent throughout, though it has been found in minute quantities in peats both to the north and south. Beech pollen, again missing here, has been found in the peats from the Islands of Rhum and Soay, and Erdtman (1924) recorded it from the Island of Lewis. He also mentions seeing stately planted beeches growing there (Erdtman, 1932). The very few grains of willow occurred sporadically and have not been graphed.

The association of high hazel with birch and pine clearly suggests that deposition began in the Boreal period. This is surprising in a peat only four feet thick but, according to Fraser (1943), the majority of Scottish peats began to form at this time.

The N.T.P. at the base is in large quantity but, to some extent, this applies to the whole sequence, so it does not seem sufficient reason, in view of the very conspicuous hazel, to date it earlier than Godwin's Zone VI (Godwin, 1940). Nevertheless, the absence of oak at the base suggests that peat formation began early in VI. The end of this period is signalized by the rise to high values of the alder curve and the line has been drawn at the level where its percentage is equal to that on the falling pine curve. The succession elm, oak, alder, is not as clearly marked here as in some neighbouring profiles, largely due to the extremely small amount of oak present. This suggests that it had not yet arrived on the island, since at a later date a figure of 20% is reached. The two preliminary small peaks in the alder curve have been seen on other profiles, notably of a very much deeper and earlier peat from Raasay. Successive hazel maxima in this zone are again quite characteristic of Hebridean peats.

Zone VII has next to be considered. A layer of highly humified peat occurred in the neighbourhood of 50 cm. depth and at the same time there is a drop in the N.T.P. before its final rise to very high values. On the basis of these two features the upper limit of the zone is drawn here. This probably corresponds to the 'Grenzhorizont' of continental writers though its discontinuity upwards is not as sharp as expected. With this limit Zone VII is relatively less in depth than is usual farther south but is in agreement with results from neighbouring islands. The peak of hazel at the junction between VII and VIII was also found in several peats from S. Uist. Successive maxima for pine, elm and oak are a feature of this diagram, the high oak reaching into Zone VIII. Towards the top of the peat these trees are very poorly represented while birch, alder and hazel remain at high percentages. As the relative frequency of alder pollen does not correspond to the present status of the tree on the island Dr Godwin made the suggestion that perhaps the peat had ceased to grow. This led to an investigation of the upper layers of the neighbouring

6 ft. cutting which was covered with a flourishing moorland vegetation and the results revealed that the suspicion was justified. The samples examined were quite similar to those of the original profile, with the exception of the uppermost which was strikingly different: it contained much less tree pollen and showed a jump in the pine curve to 65% leaving both birch and alder at the low figure of 13% though hazel only fell to 57%. A similar sudden rise of pine has been observed in varying degree in a series of profiles from S. Uist and is also to be seen conspicuously in the graph given by Fraser (1943) to illustrate the succession on the Scottish mainland. In his text he mentions that hazel, birch and alder give way to pine near the surface and attributes the change, first, to the using of the former trees for fuel and, secondly, to the planting of pines.

On Barra hazel and birch are now very rare but a few trees are to be found in the neighbourhood of Lochan nam Faoillean. Alder, oak and pine are to be found in small amounts in plantations farther north and some of the pines may just possibly be native (Forrest, Waterson and Watson, 1936 and Harrison, 1940). These trees could possibly account for the pollen found, but as the pine-rich uppermost sample was not quite at the surface of the peat the pollen may have been produced by trees which have now disappeared or, on the other hand, may have been supplemented by a general pollen rain from distant sources.

In view of this last possibility it would be rash to assume the presence of any given tree, such as lime, on an island from the evidence of very small quantities of pollen in the peat but this does not interfere with the general conclusion, reached from comparatively rich deposits of pollen ascribed to zone VII, that quite considerable numbers of forest trees grew on the better drained parts of the island during that period.

SUMMARY

A sample profile is described from a 4 ft. blanket peat from the island of Barra, Outer Hebrides.

Non-tree pollen and spores show extremely high values throughout the diagram. Only at one level, near the base, is the figure for ericoids alone less than 100%. This suggests that at no time during the deposition of the peat was there a very extensive forest cover on the island. The top and bottom of the diagram show a great preponderance of heather over all else, though in the middle there were clearly many more trees than at present.

The tree pollen diagram shows consistently high values for birch and hazel. Pine is fluctuatingly high in the earlier periods and alder, having reached a high figure, remains at 40–50% throughout. Elm and oak reach a maximum of 20%, the one early the other late in the profile.

The deposition is believed to have originated near the beginning of the Boreal period and to have continued almost to the present day.

A supplementary sample from a nearby peat showed that an uppermost layer with a high pine percentage was missing from the profile figured.

Zones VI, VII and VIII of Godwin's classification of the English peats seem to be represented and to show, in general features, a considerable resemblance to their southern counterparts.

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ZINC POISONING OF WILD PLANTS FROM WIRE NETTING

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In June 1936 two 1 m. quadrats of mountain pasture were mapped by students of Reading University and enclosed in cages of wire netting against sheep. The changes in the vegetation after two years have been briefly described (Harris, 1939). The quadrats have been remapped in 1943, 1944 and 1945, and the changes in the vegetation have been recorded. These changes appear to be due in part to the exclusion of sheep and in part to a direct harmful action of the cages which apparently poison the plants with zinc.

Both quadrats are on the north side of Cader Idris, north Wales, close to Llyn Arran and are at a height of about 500 m. O.D.

One, the '*Lycopodium* quadrat', is on a stabilized scree with a thin cover of peaty soil; the other the '*Juncus-Nardus* quadrat' is on rather deep peat, a remnant of an old blanket bog. The vegetation of the '*Lycopodium* quadrat' originally consisted of a close-grazed mossy turf about 2 cm. high, consisting of *Vaccinium myrtillus* L., *Festuca ovina* agg. sp., other vascular plants and various mosses and lichens which together made up about half the ground cover. The chief mosses are dwarf *Polytrichum commune* L., *Sphagnum acutifolium* Ehrh., *Rhacomitrium lanuginosum* Brid., *Hylocomium loreum* B. & S., and smaller amounts of several other common species including *Dicranum scoparium* Hedw.; the chief lichen is *Cladonia sylvatica* Hoffm. In this dwarf turf there are many conspicuous club-mosses: *Lycopodium alpinum* L., *L. clavatum* L. and a few *L. selago* L. There are, in addition, suppressed specimens of several flowering plants, including *Aira flexuosa* L. (*Deschampsia flexuosa* Beauv.), *Galium saxatile* L., *Potentilla erecta* Hampe. (*P. tormentilla* Neck.) and a very little *Calluna vulgaris* Salisb., which is so small that its detection requires close search among the moss.

The '*Juncus-Nardus* quadrat' was dominated by *Nardus stricta* L. and *Juncus squarrosus* L. in almost equal amounts. These plants have stiff leaves which point upwards and outwards to form rosettes with raised and overlapping edges about 5–10 cm. high. The inner parts of the rosettes have no other plants, but at the edges there are a good many flowering plants and mosses in a suppressed condition. The mosses are the same as those mentioned in the '*Lycopodium* quadrat'. There is no *Lycopodium* in this vegetation, but many small *Vaccinium myrtillus* shoots occur. *Aira flexuosa* is minute and hard to find, and there happened to be a shoot of *Empetrum nigrum* L.

The vegetation around both quadrats has proved to be fairly stable, having undergone no obvious change in these six years. The chief changes in the enclosed quadrats after the first two years were as follows. In the '*Lycopodium* quadrat', *Vaccinium* grew up to 10 cm., and among its shoots the grasses came into flower, the *Lycopodium* plants diminished and so did *Galium saxatile*, and *Potentilla erecta* and the mosses and lichens had vanished. A *Calluna* shoot had formed a promising little bush. In 1944 the *Vaccinium* was completely dominant and very fruitful, except in one part of the quadrat

where *Calluna* grew above it. Grasses (now chiefly *Aira flexuosa* and *Festuca ovina*) were less abundant than in 1938. In 1945 all the *Vaccinium* looked unhealthy and there are a good many dead shoots, particularly near the wire fence at the sides of the quadrat and for the first time some bare soil is to be seen. *Calluna* is still growing well and a single shoot of *Lycopodium alpinum* survives. No *Galium*, or *Potentilla* remains, and no moss or lichen has come back (except for loose fragments, obviously blown in recently).

The '*Juncus-Nardus* quadrat' developed rather differently. *Aira flexuosa* became dominant and has progressed to form an astonishingly thick leaf mat 10–30 cm. high, which excludes everything but *Vaccinium* (subdominant) 20 cm. high and some sturdy *Empetrum* branches on top of the mat. A single plant of *Nardus* survives, but not one of *Juncus squarrosus*, *Galium*, *Potentilla*, moss or lichen.

There is no vegetation on Cader Idris resembling the '*Juncus-Nardus* quadrat' in its present condition, but there is some which has much in common with the '*Lycopodium* quadrat'. This is on large boulders which have fallen from the cliffs, and some of these boulders have vertical sides inaccessible to sheep and a flat top where up to 10 cm. of peat has formed and supports a little garden of ungrazed heath. *Calluna* is usually dominant and about 15 cm. high; *Vaccinium myrtillus* subdominant and about 10 cm., and there is much *Aira flexuosa*. Sometimes there are strong clumps of *Molinia caerulea* Moench. and sometimes wind-blasted shoots of *Pyrus* (*Sorbus*) *aucuparia* L. growing about 20 cm. high. *Lycopodium* does not occur. A very striking difference from the quadrat is that all the mosses and lichens of the surrounding grassland grow here abundantly both in the shelter of *Calluna* and in the open.

These naturally protected areas show that the disappearance of the mosses and lichens in the quadrat is not due to the mere absence of sheep grazing. It was thought possible that the wire netting of the cage might have exerted a direct effect, and accordingly, in 1944, a typical sample of the *Lycopodium* grassland close to the quadrat was covered with a wire-netting roof supported by corner stakes as in the fenced quadrats, but with fully open sides so that sheep could easily graze underneath. In 1945 this vegetation showed no change as far as the vascular plants are concerned, all species appearing healthy and just as close grazed as elsewhere. The bryophytes and lichens, however, had suffered devastation. *Sphagnum* formed dark grey cushions, *Hylocomium loreum*, *Hypnum schreberi* Willd., *Dicranum scoparium* and *Rhacomitrium lanuginosum* were dirty yellow and *Cladonia* had all disappeared, presumably having rotted quickly after death. The only living bryophyte was *Polytrichum commune*, and this was dead up to near the apex. This makes a clear contrast with the vegetation elsewhere where nearly all the moss was alive and healthy; only scattered plants are failing or dead. The killing of the moss extends a little way outside the shelter of the roof, but nowhere more than 50 cm. from it. It is suggested that the killing is due entirely to toxic matter—probably zinc hydroxide removed by raindrops on the zinc coating of the galvanized iron wire, and dripping from the roof or blown outwards at the sides.

Poisoning of plants by zinc is supposed to be rather uncommon and has not been very much investigated (Brenchley, 1927). It is known that different species have very unequal tolerance, some (e.g. barley) being appreciably harmed by culture solutions with as little as one part of zinc in 1–2 millions, and quickly killed by a higher concentration; others, particularly certain weeds, found in soils containing zinc carbonate are very tolerant

and accumulate large amounts in their tissues. Crops have been poisoned by soils grossly contaminated by industrial zinc refuse (Knowles, 1945).

Crops are often grown in cages of galvanized wire to protect them from birds, and the results are said to be generally satisfactory though I have no experience of such work. Dr Brenchley, however, informs me that failure in such cages has occasionally been noted and has been attributed to the zinc. For this reason such cages at Rothamsted are painted.

It should perhaps be pointed out that a number of crop plants have been shown to benefit from a small amount of zinc, and while it may be true that they, and perhaps all plants, need zinc as an essential element for life, they need very little indeed. One part of zinc in 50 millions gave full benefit in a water-culture experiment with peas (see Brenchley, 1927), but the minimum for healthy growth was not determined. The poisonous concentrations discussed in this paper are hundreds of times greater than these nutritional concentrations.

Some experiments show that (*a*) appreciable amounts of zinc are removed by water from galvanized wire, and (*b*) that this water kills certain plants.

Pieces weighing 100 g. of fairly new and very old wire netting were tightly rolled up and placed in flasks with 100 c.c. of distilled water at laboratory temperature (about 20° C.) and loosely corked. In cutting and rolling up the wire a certain amount of the iron was exposed. In the old blackish wire netting which had been weathered for 9 years and possibly longer, some of the zinc had gone and the iron had rusted in places and even corroded away. Almost at once a distinct smell was noticeable with both samples (as when a metal is dissolved in dilute acid), and before long the water grew cloudy and was very milky in 24 hr. About equal turbidity was generated in each subsequent 24 hr., and the turbidity with tap water (calcareous) was about the same as with distilled water. The precipitate appears to be zinc hydroxide, and as it is appreciably soluble the water becomes distinctly alkaline. Both samples were extracted for several days, the water with zinc hydroxide being replaced by fresh distilled water daily. Then after a week of this treatment the weight of zinc extracted in 24 hr. was determined. It proved to be 51 mg. from 100 g. of the new wire and 33 mg. from 100 g. of the old. At this rate the new sample would have lost all its zinc in about a year. The total amount of zinc concerned is impressive. The 'new' sample is almost 20% zinc, and 100 sq.cm. yielded 6·0 g. of zinc—almost 2 tons per acre.

This water, containing about 500 parts per million of zinc is, as would be expected, very toxic. Ten similar samples of *Sphagnum acutifolium* were put in beakers; five were watered with this zinc liquor and the others with distilled water, but afterwards they were all watered with distilled water. The plants with the zinc were distinctly discoloured after 6 days, and after 8 days the branches were all greyish and dead, though the terminal buds were still green. The five control plants remained healthy in appearance. A few small flowering plants accidentally included still appeared healthy. Admittedly both the conditions of corrosion and of poisoning are extreme, but they prove the possibility of this poisoning.

According to Evans (1926) only the surface layer of galvanized iron is pure zinc (which has the familiar grey colour), the bulk of the cover is made of iron : zinc alloys (which appear dark grey, nearly black when weathered). The pure zinc is more quickly corroded by water and also by NaOH than the alloy. With this 'new' wire netting, after

the surface has been corroded for some weeks by water, it was further corroded by alkali when it was nearly all of the blackish colour. It then yielded rather less zinc to distilled water in 1 day, namely, 34 mg. instead of 51 mg., almost the same as what the old sample yielded.

It was also noted that there is no rusting at all of exposed parts of the iron, while plenty of the zinc is present elsewhere, but after the surface has reached the black under-layer, rusting is perceptible, and the zinc precipitate in the water begins to be stained by iron. Of course, after all the zinc is removed by acid from the superficial zinc : iron alloy, rusting of the bare iron proceeds at a very rapid rate. We should thus expect that the supply of zinc through corrosion would gradually fall off to some extent.

The corrosion of zinc in oxygenated water is regarded as an electrolytic action. In the presence of an electrolyte and of iron which acts as a cathode, the zinc dissolves as the anode. The iron is not, however, necessary, for an oxygenated solution of KCl will corrode pure zinc. Here minute pores and scratches which are shielded from oxygen act as the anode and corrode actively, and so large pits are eaten out under a thick coat of zinc hydroxide, while the exposed, oxygenated areas remain uncorroded and bright (Evans, 1926). Even the KCl is unnecessary; the zinc hydroxide will apparently serve as the electrolyte, though in my experiments I found the rate of corrosion just over ten times quicker in the presence of KCl.

The rate of corrosion of zinc from the galvanized wire under ordinary conditions of weathering was not studied. In ordinary dry air it is certainly very slight indeed, almost negligible, but I cannot say how intermittent drying would affect the rate of corrosion during wet periods. No doubt the presence of electrolytes would increase the rate while grease and dirt might decrease it. Evans found that sulphur dioxide in the presence of water vapour causes considerable corrosion and this might materially increase the rate in the heavily contaminated air, but the rate caused by pure water is so high that its additional effect should be very slight in ordinary air. In the very pure air of north Wales it must be negligible, as it certainly is in the flasks of distilled water.

I regret that no analysis of the wire used for the Cader Idris quadrats can be given, the original net not being available. It was of wider mesh than the 'new' sample and so would yield a good deal less zinc than 2 tons per acre, but still, no doubt, a substantial amount of this very poisonous metal. By no means the whole of the zinc has yet been corroded from it (that is after 6 years' exposure), though the black under-layer is now exposed, and there is some rusting of the iron, but the rusting is only local and nowhere severe.

Let us return to the quadrats. It is clear that the results in the vegetation of the quadrats are a mixture of the effects caused by protection from grazing and the killing effect of zinc poisoning. The vigorous growth of the heather or grass is doubtless due to the protection, and the rapid death of the moss due to poisoning, but whether the slow decline of various vascular plants is due to poisoning or competition or partly both cannot be said. Thus the experiment has proved to be of wrong design.

Farrow (1916, 1917) performed experiments on the rabbit-grazing of various kinds of heath in East Anglia by enclosing small samples in wire-netting cages, and the idea of the present fenced quadrats was taken from his work. *Calluna* and various other flowering plants which were grazed almost to death outside grew vigorously in his enclosures, but he does not deal with the fate of the small mosses and lichens formerly

covering the ground. He mentions (1916, p. 62) that *Cladonia* disappears and attributes this to smothering; the present work suggests that it may have been poisoned.

For future experiments this poisoning could be avoided by having no roof over the enclosed area, and a side fence high enough to prevent any animal jumping in and distant enough to prevent drops of water blowing in from it. It is hoped that such an experiment will be set up soon.

In any fencing experiment where a roof is necessary, galvanized wire protected by bitumen would no doubt be satisfactory as a rule, since the supply of zinc would be reduced to below the toxic level. Where the fate of specially susceptible plants such as mosses and lichens is concerned, however, it might be better to use nickel netting, since it would be difficult to test the efficiency of the bitumen cover under conditions of weathering.

The poisoning of vegetation from galvanized wire raises a different question: whether water which has stood in a galvanized iron tank and watering-can is ever dangerous. I found that the rain-water which I had used for various plants in a greenhouse contained 6 parts of zinc per million—an amount which would kill certain plants in water cultures. Dr Hewitt has informed me that rain-water stored in galvanized iron tanks at Long Ashton contained as much as 15 parts per million of zinc and proved deadly to sugar-beet in sand culture.

In the Cader Idris experiments all the mosses and *Cladonia* proved more susceptible than all the vascular plants. This might be anticipated. The mosses and lichens concerned, except for *Polytrichum* which is least susceptible, grow resting on the turf and soil rather than rooted in it. They can receive little protection from the zinc by any soil precipitation that may occur. Moreover, they are plants which must normally be nourished by exceedingly dilute solutions of essential nutrients, and for such plants a solution of several parts per million of a poisonous substance might well be particularly devastating.

I have found in attempts to grow various wild plants, chiefly bryophytes, at Reading that the species which are found wild on neutral soils have usually proved easy to grow, those which grow on acid peats were more difficult, while those which grow wild with the minimum of nutrients (as on hard rocks and on tree bark) were quite impossible. It now seems very likely that much of my difficulty may have been due to the use of this rain-water contaminated with zinc. Dr Hewitt has been good enough to tell me a remedy—to paint the tank and watering-can inside with paint of pure bitumen, when the zinc content of the water is reduced to well under 1 part per million. There is a difficulty in painting galvanized iron (Duncan, 1934). In its manufacture the cleaned iron is immersed first in zinc chloride, then in molten zinc covered with tallow, and as it emerges is coated with grease and zinc oxychloride. This grease clings to it persistently, and apparently the only effective way of removing the grease and the oxychloride is to expose the galvanized iron to weathering for a year. After weathering the galvanized iron takes the paint very well.

Experiments are being started with various mosses, *Drosera*, and other plants of botanical interest but reputed difficult to grow, in which one set is to be supplied with this rain-water, and the other set with the same water to which the zinc is added to the amount normal in a galvanized tank.

The botanical part of this work was done with the help of students and staff of the Reading Botany Department. It is a pleasure also to acknowledge help from Dr W. E. Brenchley of Rothamsted, Dr E. J. Hewitt of Long Ashton and Dr G. H. Cheeseman of the Chemistry Department, Reading University.

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OBSERVATIONS ON SOIL ALGAE

I. THE ECOLOGY, SIZE AND TAXONOMY OF BRITISH SOIL DIATOMS

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(With 18 figures in the text)

PART 2

CONTENTS

F. TAXONOMY

The following are new records for Great Britain:

Eunotia exigua (Bréb.) Grun. f. *linearis* Krasske.
Neidium minutissimum Krasske.
Stauroneis truncata n.sp.
S. thermicola (Boye Pet.) n.com.
S. Borrichii (Boye Pet.) and var. *subcapitata* Boye Pet.
Navicula ignota Krasske. Emend. and vars. *palustris* Hust. and *anglica* n.var.
N. Heufleriana (Grun.) Cleve var. *minor* n.var.
N. Brockmanii Hust.
N. Vaucheriae Boye Pet. and var. *densistriata* n.var.
N. pseudagrestis n.sp.
N. Fritschii n.sp.
N. fossalis Krasske.
N. muralis Grun. f. *agrestis* (Hust.)
N. cryptocephala Kütz. f. *terrestris* n.f.
N. tenelloides Hust. Emend.
Pinnularia saxicola n.sp.
P. silvatica Boye Pet.
P. subcapitata Greg. var. *constricta* Hust.
Amphora montana Krasske.
Cymbella microcephala Grun. f. *sublinearis* n.f.
Nitzschia parvula Lewis var. *terricola* n.f.
N. communis Rabh. var. *hyalina* n.var.
N. terricola n.sp.

The following are new species previously recorded under the names given in brackets:

Stauroneis Muriella (*Navicula pupula* Kütz.).
Navicula pseudatomus (*N. atomus* Grun.).

Consideration of the species observed

Eunotia Ehr.

Small specimens, relegated with difficulty to definite species, occurred on five acid woodland and one moorland soil. Geitler (1932) has shown for *E. formica* Ehr. that the smallest cells of a clone lose the specific characteristics (e.g. compare his fig. 38 *c–f* with figs. 36 and 37). Species of *Eunotia* often occur in the tufts of the less xerophytic mosses (Beger, 1928; Krasske, 1932; Hustedt, 1938, 1942). The soil species, like the majority of the aquatic ones, appear to be calcifuge and may be recruited from moss tufts since they never occurred in quantity.

(1) *Eunotia exigua* (Bréb.) Grun. f. *linearis* Krasske (1932, fig. 5*d*). Fig. 2 A, B

13–15 μ l.; 3 μ br.; 20–25 str. in 10 μ. From an eroded bank on the edge of an oak copse (S35). Valves of similar shape occur in *E. praerupta* Ehr. (Hustedt, 1930, p. 174, fig. 211), the forma described by Krasske (1932, fig. 3) and var. *muscicola* Boye Pet. (Petersen, 1928, p. 377, fig. 3) of *E. praerupta*, but all differ in the much less dense (6–15 in 10 μ), coarser and more irregularly spaced striae and, generally, much larger size.

(2) *Eunotia tenella* (Grun.) Hust. Fig. 18 F–I

A few specimens occurred on two woodland soils (S20, E), some (Fig. 18 F, G) clearly belonging to this species (18–25 μ l.; 4 μ br.; 17–18 str. in 10 μ), together with others which differed in showing little or no decrease in the width of the valve towards the apices (Fig. 18 H, I, 9–12 μ l.; 3 μ br.; 17–18 str. in 10 μ). These latter show some resemblance to the cells of 'minimal size' obtained by Geitler (1932, p. 78 et seq., figs. 38*h*, 39*h*) in cultures of *E. formica* Ehr., and, as in that species, the simplification of the valve outline may be related to the decrease in size.

(3) *Eunotia praerupta* Ehr. forma. Fig. 2 C, D

10–15 μ l.; 4–5 μ br.; 16–18 str. in 10 μ. In enriched samples from one woodland soil (S46). The striae are more numerous than usual, suggesting a transition to the forms of *E. tenella* described above. The dorsal margin of the larger specimens is weakly indented centrally, as in var. *bidens* Grun. (Hustedt, 1930, fig. 213).

(4) *Eunotia pectinalis* (Kütz.) Rabh. Fig. 2 E, F

20–31 μ l.; 3 μ br.; 15–17 str. in 10 μ. The soil specimens agreed with the species in the incurved dorsal margin close to the apex of the valve, and the almost parallel course of the dorsal and ventral margins, though in size, they approach var. *minor* (Kütz.) Rabh. The density of the striae is not recorded for this var. by Hustedt (1930, p. 182), but, by inspection of his fig. 238 (p. 181), is approximately 15 in the centre and 18 in 10 μ near the apices. 7–12 str. in 10 μ are recorded for the species by him, but, from measurements of his fig. 237, this is only the case in the central portion of the valve and, near the apices, there are approximately 16 in 10 μ.

The dorsal margin is flat according to Hustedt (1930), but, in Geitler's (1932) cultures

(fig. 46, p. 87), greater convexity occurred than in this form. The arching of the intercalary bands and girdle, characteristic of this species, has been shown by Geitler (1932) to enable it to subdivide without the regular decrease in size customary for diatoms.

Not observed alive but present on slides from an acid woodland (S 14) and an acid moorland soil (S 22).

Achnanthes Bory

(5) *Achnanthes minutissima* Kütz. var. *cryptocephala* Grun. Fig. 2 G–K

In the soil specimens (6–13 μ l.; 2–3 μ br.; 30–35 str. in 10 μ) the short central striae of the raphe-bearing valve are not only more prominent but also stand farther apart than the rest, a feature shown in Van Heurck (1899, pl. 8, fig. 334*b*) and Grunow's figure in Van Heurck (1880–5, pl. 27, fig. 43) and found by Dr Butcher (private communication) in specimens from various rivers.

Present on six soils, but live cells were very rare so that it is only doubtfully euterrestrial. McCall (1933, p. 226) has recorded it from a porcelain sink in a greenhouse and, like Beger (1928), I have occasionally found specimens in tufts of xerophytic mosses. Petersen (1928, 1935), who likewise found it among mosses in Iceland, considers it to be, at the most, pseudo-aerial.

Frustulia Thwaites

(6) *Frustulia vulgaris* Thwaites. Fig. 2 O, P

34–42 μ l.; 8–9 μ br.; approx. 28 str. in 10 μ. Present on seven soils, but only in three of them were live frustules seen (S 5, 31, 30); in each case *Cylindrospermum* was also abundant, in the strata of which alone were the typical mucilage tubes observed. Hustedt (1942) records it from mosses.

Caloneis Cleve

(7) *Caloneis fasciata* (Lagerst.) Cleve (incl. *Navicula fontinalis* Boye Pet.; Petersen, 1915, p. 286). Fig. 2 L, M, Q–T

There is considerable confusion concerning the diatoms here grouped. Petersen (1928, p. 382 et seq.) has described a number of forms whose valves have in common a transapical fascia and 23–27 str. in 10 μ, often all parallel. These may or may not possess distinct apical lines which generally appear as a row of dots on the striae (e.g. Petersen, 1928, fig. 8) and he has criticized (1935, p. 141) Hustedt (1930, p. 316), who places the linear-lanceolate forms with apical lines in *Caloneis bacillum* (Grun.) Mereschk. and the linear-lanceolate forms without visible apical lines and sometimes weakly rostrate apices in *Pinnularia fasciata* (Lagerst.). Petersen does not mention, however, that *Caloneis bacillum* sensu Hustedt has all the striae radial, except the central ones which may be more or less parallel, while *Pinnularia fasciata* sensu Hustedt has parallel or weakly radial central striae and weakly convergent apical striae. In Lagerstedt's original description and figure (*Navicula fasciata*, 1873, p. 34, pl. 2, fig. 11 *a*) the striae are all parallel. It would appear that there are two separate species differing in their striation and that *Pinnularia fasciata* sensu Hustedt consists of specimens in which the apical line is not clearly visible. Hence, some of Petersen's (1928) forms (e.g. var. *elliptica*) seem to belong to *Caloneis bacillum* (see also Cleve, 1894–5, pt. 1, p. 50).

All the valves seen by me (10–30 μ l.; 4–7 μ br.; 23–28, in the smallest cells 30 str. in 10 μ) were linear-lanceolate to lanceolate, except the smallest which were elliptical

(Fig. 2 T), with the central striae parallel and the apical ones weakly convergent or, in the smallest cells, also parallel. Some of the striae may be curved with the concave surface facing the apex of the valve (Fig. 2 L, M). The fine apical lines were sometimes visible as a row of dots along at least part of the valve. A curious feature is that the largest specimens generally have the faintest striations (cf. Petersen, 1928, p. 383). The branches of the raphe both curve towards the same side of the valve in the region of the central nodule. I am retaining these specimens in *C. fasciata* (Lagerst.) Cleve.

This is one of the few diatoms characteristic of highly acid soils deficient in phosphates and nitrates, being present on seven moorland and woodland soils (S 18, 22, 25, 27, 33, 35, 46). Petersen (1935, p. 142) records it on cultivated soil in Denmark but does not particularize which of his forms this is.

Neidium Cleve

(8) *Neidium bisulcatum* (Lagerst.) Cleve

28–29 μ l.; 5–6 μ br.; approx. 30 str. in 10 μ. Observed in preparations from an enriched sample (S 10). Probably not a soil diatom.

(9) *Neidium minutissimum* Krasske (1932, fig. 12). Fig. 2 N

The few soil specimens (17 μ l.; 5 μ br.; 21 str. in 10 μ) occurring in a preparation from one soil (S 21) agreed with Krasske's in the linear valves and the elongated processes from the central pores. The valves, however, were barely triundulate and almost constricted centrally, while, though most of the punctate striae were radial, a few irregularly placed convergent ones occurred. Previously recorded from calcareous rocks which also occurred near this soil.

Stauroneis Cleve

(10) *Stauroneis anceps* Ehr. Fig. 3 I, J

A few specimens (26–34 μ l.; 7–8 μ br.; 26–27 str. in 10 μ) of the species and f. *linearis* (Ehr.) Cleve (Fig. 3 I) occurred on two woodland and one garden soil (S 20, 21, 30). A small form of this species is recorded from Greenland soil (Petersen, 1935).

(11) *Stauroneis truncata* n.sp. Fig. 2 U–AA

Valves (12–30 μ l.; 4–5 μ br.; 25–30 str. in 10 μ) linear with or without a weak central constriction or a weak central concavity on one side of the margin only. The apices of the larger valves are truncate or weakly rostrate, of the smaller cells truncate. There is every gradation between concave and plane margins and between rostrate and truncate apices. In the smallest specimens (Fig. 2 AA) the apices are so weakly truncate that the valves are linear-elliptic. The axial area is narrow, the central area a wide stauros. The branches of the raphe are straight. The striae are all radial, the more central curved, and one or more of the four bounding the stauros shorter than their neighbours.

This species differs from the very variable *S. anceps* in the rostrate-truncate apices and the sometimes centrally constricted valves. *S. agrestis* Boye Pet. (Petersen 1915, p. 289, fig. 9), which may be a variety of *S. anceps*, also possesses linear valves with weakly constricted margins but differs from *S. truncata* in the sharply narrowing and capitate apices.

Present in small numbers on a woodland soil (S 10).

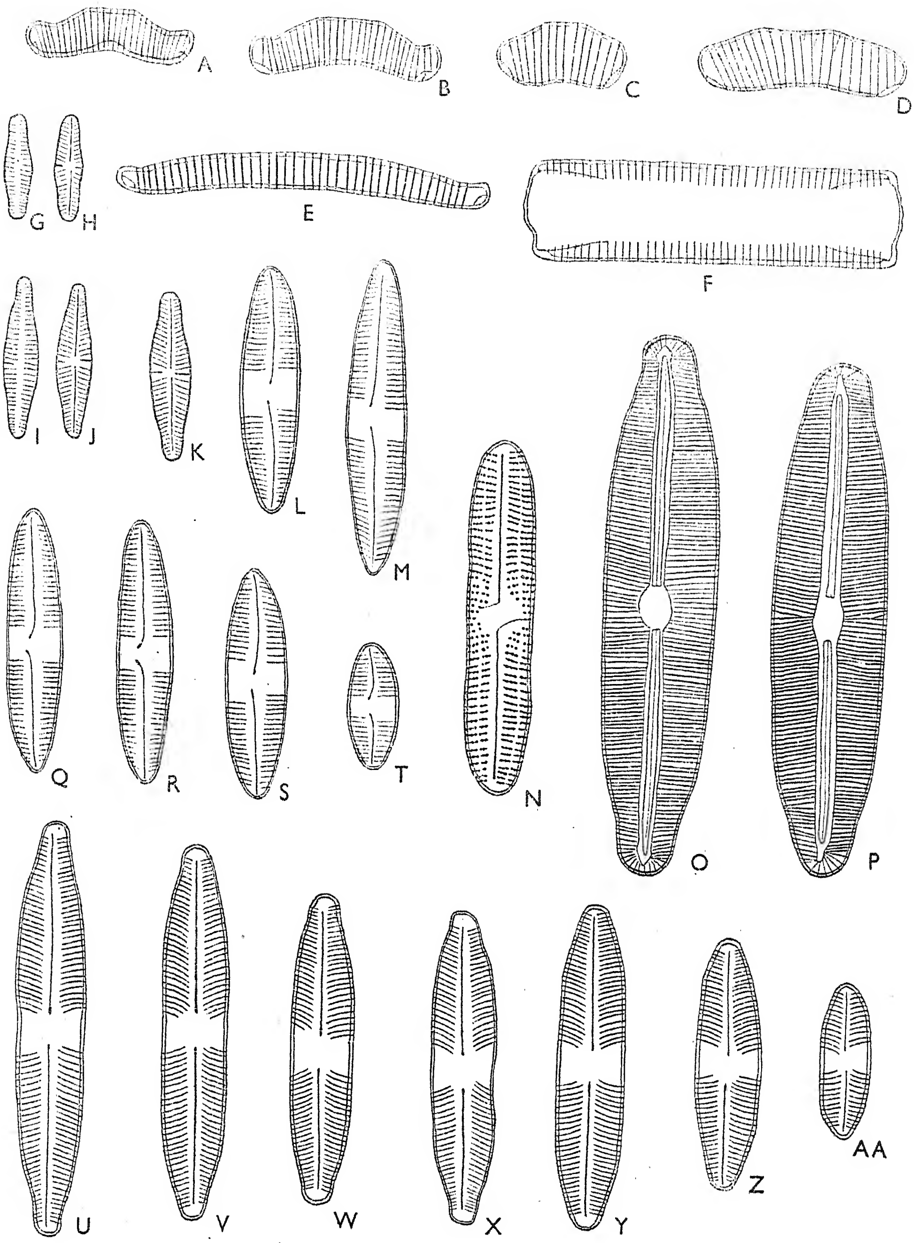

Fig. 2. A, B, *Eunotia exigua* (Bréb.) Grun. f. *linearis* Krasske; C, D, *E. praerupta* Ehr. forma; E, F, *E. pectinalis* (Kütz.) Rabh.; G–K, *Achnanthes minutissima* Kütz. var. *cryptocephala* Grun.; L, M, Q–T, *Caloneis fasciata* (Lagerst.) Cleve; N, *Neidium minutissimum* Krasske; O, P, *Frustulia vulgaris* Thwaites; U–AA, *Stauroneis truncata* n.sp. All ×1750. In this and succeeding figures all the drawings are of valves except where stated (e.g. 2F, girdle view).

(12) *Stauroneis thermicola* (Boye Pet.) n.com. (*Navicula thermicola* Boye Pet.; *Stauroneis montana* Krasske; *Navicula contempta* Krasske). Fig. 3 K–AA

It is not wholly clear whether the diatom here described should be considered under this species or under *N. thermicola* Boye Pet. (Petersen 1928, p. 394), from which it differs in the presence of what appears to be a stauros and not a transapical fascia. Apart from this, *N. thermicola* only differs from *Stauroneis montana* Krasske in that the latter is said to show the beginnings of septum formation (Hustedt, 1930, p. 259). Petersen (1935, p. 143) states that the two species are very similar and that Krasske has verified that his *Navicula contempta* is the same as *N. thermicola*. *Stauroneis montana* is only figured in valve view (Hustedt, 1930, fig. 418), where the incipient septum appears as a dark line close up against the apex. *Navicula thermicola*, when seen in girdle view (Petersen, 1928, fig. 20), shows, what Petersen calls, terminal nodules drawn out into apical costae. Many of my specimens, though not always clearly, show the valve view described for *Stauroneis montana* (Fig. 3 R–T), and all show the girdle view described for *Navicula thermicola* (Fig. 3 Y). It is not clear by what means the costae of Petersen may be distinguished from the incipient septa of Krasske. I am of the opinion that the dark line sometimes seen near the apex of the valve is due to the costae seen in girdle view. These latter are not septa but structures similar to those in *Stauroneis Borrichii* (q.v.). Besides the stauros, the punctate radial striae are characteristic of *Stauroneis*.

The larger cells usually have valves (11–16 μ l.; 3–4 μ br.) with parallel or weakly convex margins (Fig. 3 K–M, R–T) and decrease sharply in size near the capitate, subcapitate or broadly rostrate apices. With decrease in size, the valves (approx. 8–10 μ l.; 2·5–3·0 μ br.) become less markedly linear (Fig. 3 N–Q, V–X) and less markedly narrowed near the now rostrate apices. Less commonly the valves are narrowly capitate or rostrate (Fig. 3 T, Z, AA), while the margin on one side may be concave centrally or the valve may be centrally constricted (Fig. 3 U, AA). Narrow rostrate apices and slightly convex margins, where combined (e.g. Fig. 3 Z), give the valves a more slender appearance, and such valves are often very slightly narrower (approx. 0·5 μ) than the typical forms. These more lanceolate forms are doubtless identical with var. *lanceolata* Hustedt (1935, p. 381).

The various valve shapes all pass into one another and occur intermingled with the typical forms, so that they do not appear to be separate varieties. Hustedt (1942, p. 72) has, however, pointed out that var. *lanceolata* is not composed of valves showing simplification with decrease in cell size, and this is true of the larger rostrate valves of the soil specimens (e.g. Fig. 3 Z). As all the small valves are rostrate it is not possible to determine from which type of valve they have arisen.

The branches of the raphe are always straight and the axial area very narrow, widening abruptly into the central stauros. The striae (24–30 in the larger and 25–35 in 10 μ in the smaller cells) are all radial. The central striae are more clearly punctate and less dense (approx. 20–25 in the larger and 25–30 in 10 μ in the smaller cells) than those near the apex (30 and more in 10 μ); in the more robust valves the central ones are clearly curved (Fig. 3 K, R).

The species, present on twenty-six soils, is common on garden and other well-cultivated soils which are somewhat acid or nearly neutral but rarely occurs in quantity.

var. *elongata* n.var. Fig. 3 BB–JJ.

On one woodland soil (S 10) there occurred cells differing from the species in their

var. *subcapitata* Boye Pet. (Petersen, 1915, p. 285, fig. 3). Fig. 3 A, B

As in Petersen's specimens, the valves are robuster than in the species (23–26 μ l.; 6·0–6·5 μ br.; str. 19–20 centrally and up to 25 in 10 μ apically). The median constriction of the valve may be present or absent and, in the English specimens, the capitate apices are rounded; in the Danish ones they are truncate. The apical area free of markings is more marked than in the species or, in the larger specimens, than in Petersen's specimens of this variety. As no clear transitions between it and the species have been seen, it may be a good variety.

Petersen (1928, p. 388) has described a var. *undulata* with triundulate valves which is also recorded by Hustedt (1937–8, p. 237, pl. 17, fig. 7), who also places the species in *Navicula*. It may be doubted, however, whether Hustedt's specimens do belong to this species, as he neither mentions nor figures the characteristic structure of the apical portion of the surface of the valve.

As in Denmark, Iceland and Jutland (Petersen, 1935), the species and var. *subcapitata* occurred together in garden (S 53, B, C) and field (S 45) soils but were never frequent.

(14) *Stauroneis* (*Navicula*?) *Muriella* n.sp. (*Navicula pupula* Bristol non Kützing). Fig. 4 A–L

From the figures, Bristol's *Navicula pupula* and its var. *undulata* (1920, p. 69, text-fig. 9, figs. 24–28) appear to differ from Kützing's species in the absence of the lateral enlargement of the polar nodules, and the striations around the central area ('false stauros' of Bristol) are so short that they only appear within the margin (compare Hustedt's description and figures of *N. pupula*; 1930, p. 281, fig. 467). Bristol states, however, that the terminal nodules are enlarged but not to the extent that is figured by Cleve & Grunow (1880, pl. 2, fig. 53). It is possible that the intercalary bands seen in girdle view were responsible for Bristol's description (see below). The diatoms observed by me differ from both *N. pupula* Kütz. and Bristol's descriptions in that there is a central stauros, the polar nodules are not enlarged sideways, and the apical striae are either parallel or weakly convergent. It is very difficult in small diatoms to decide whether there is a stauros or a fascia, but it appears to me that the former is present here. Bristol does not describe the girdle view but, in my specimens, the pervalvar axis may be of considerable length (width in girdle view) and a number of intercalary bands are present (Fig. 4 J, L). They never separate from one another in permanent preparations, nor are they so distinct over all parts of the cell that it is possible to figure all of them completely. As in the case of the costae of *Stauroneis montana* (q.v.), these appear to give rise to the dark lines occasionally seen near the apices in valve view (Fig. 4 G), which Bristol presumably took to be the lateral enlargements of the terminal nodules. My diatom differs, therefore, from Bristol's *Navicula pupula* Kütz. in the stauros, orientation of the apical striae and the intercalary bands. In spite of these apparent differences, I have no doubt that Bristol's and my diatom are one and the same, for they agree in other features, especially the very variable and characteristic outline of the valve (see below).

The valves (12–24 μ l.; 3–4 μ br.) are always 4–6 times as long as broad. The basic shape of the valve is linear-lanceolate (f. *linearis*, Fig. 4 F, and see Bristol's text-fig. 9, fig. 24), but, in the commonest form, they are dilated centrally (Fig. 4 A–C; cf. Bristol's text-fig. 9, fig. 25). Some are triundulate (f. *triundulata*, Fig. 4 G–I; cf. Bristol's text-fig. 9, fig. 28). The apices vary from broadly rounded to more or less clearly

capitate (compare Fig. 4 A, F with B–E, G–I). The striae are finely punctate, the central ones being more prominent and less dense (approx. 20–25 in 10 μ) than those near the apices (up to approx. 30 in 10 μ). The central striae are radial and the apical ones, often difficult to see, are either parallel or very weakly convergent. The axial area is very narrow, passing abruptly into the central stauros. The fine branches of the raphe are straight.

As no clear gradations were seen between the various valve forms they are described separately as follows, all other features as described above:

Stauroneis Muriella n.sp. Fig. 4 A–C. Valves lanceolate, centrally inflated with widely rounded or more or less clearly capitate apices.

f. *capitata* n.f. Fig. 4 D, E. Valves linear-lanceolate and capitate.

f. *linearis* n.f. Fig. 4 F, K. Valves linear with rounded apices.

f. *triundulata* n.f. Fig. 4 G–I. Valves triundulate with capitate to truncate-capitate apices.

Only recorded from British soils (Bristol, 1920, eleven samples). Rarely present in large numbers, though occurring on seventeen soils and showing a preference for well-cultivated places. It also occurred on the marginal mud of a shallow woodland pool at Lapworth, Warwickshire.

Navicula Bory

The various sections into which this genus has been divided by Cleve (1894–5) are, in part, highly artificial. I have had considerable doubt into which a number of the soil forms should be placed and, so far as possible, have followed Hustedt (1930, 1937–8).

Naviculae annulatae Hustedt (1937–8, p. 254)

(15) *Navicula ignota* Krasske emend. (*N. Lagerstedti* Cleve in Hustedt, 1937–8; non *N. Lagerstedtii* Cleve 1894–5). Fig. 4 O–V

Valves (13–19 μ l.; 4–5 μ br.) linear triundulate with capitate (Fig. 4 O–Q) or rostrate-capitate (Fig. 4 T) apices. With decreasing size the valves become less markedly triundulate (Fig. 4 R, S; cf. Hustedt in Schmidt's *Atlas*, *99–100*, pl. 400, figs. 35–37) and capitate. Branches of the raphe fine and straight, apical nodules some way from the apex of the valve, the part of the axial area flanked by the characteristic apical striae always being free of any part of the raphe. Axial area narrow, central area hour-glass shaped. Striae (15–18 in 10 μ, excluding the shortened ones opposite the central nodule) thick but not very prominent, radial and curved except near the apex and opposite the central nodule. Though the striae are much thicker than in most soil *Naviculae* of the same size, they only appear as relatively pale lines and are not so prominent as black and white figures suggest. The apical striae, which are parallel and usually three on each side of the axial area, typically consist of two parts, and the area between them forms a more or less clear semicircle (Fig. 4 O, V). However, the most apical ones are often composed of one shortened portion (Fig. 4 P–R), and the line between those of two parts may diverge from a semicircle (Fig. 4 P–R). This line seems to be due to an absence of markings and not to any other longitudinal line crossing the striae. The most apical striae may not only consist of one shortened portion but also be radial (Fig. 4 P–R). There are one, two or, rarely, three short parallel striae opposite the central nodule. These are shorter than the radial striae and stand at some distance from them. They may be of unequal length (Fig. 4 Q). The more rostrate larger valves have

somewhat thinner striae and only one shortened stria opposite the central nodule (Fig. 4 T–V). These may belong to a separate form, but they always occurred with the type and some of them came very close to it.

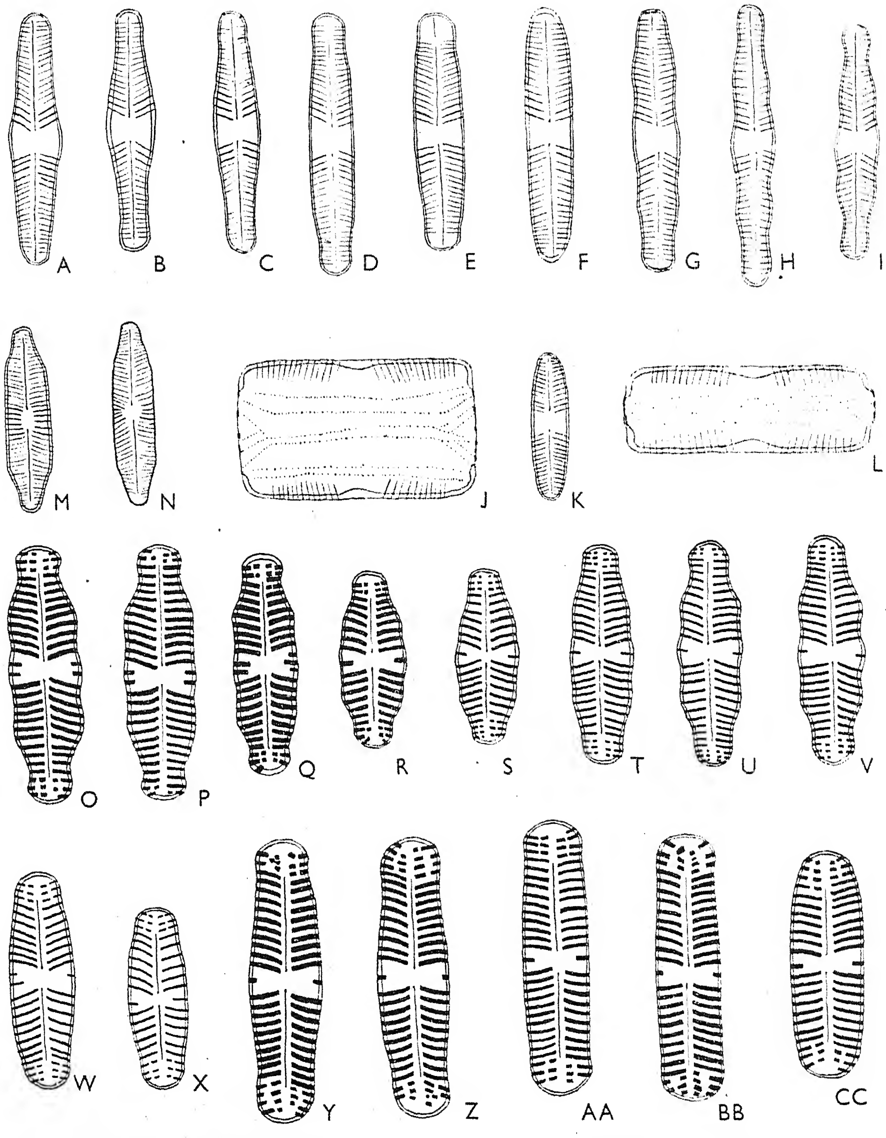

Fig. 4. A–L, *Stauroneis Muriella* n.sp.; M, N, *Navicula Brockmannii* Hust.; O–V, *N. ignota* (Krasske) emend.; W, X, ibid. var. *anglica* n.var.; Y–CC, ibid. *palustris* Hust.; J, L, girdle views. In C, E, the more apical striae are not shown. All × 1750.

Krasske's original description (1932, p. 116, pl. 3, fig. 19) differs in the greater maximum size of the valves (17–25 μ l.; 4·5–5 μ br.) and less dense striation (12–14 in 10 μ); the branches of the raphe reach almost to the apex of the valve and the apical striae are unbroken. Hustedt (1937–8, p. 254, pl. 18, figs. 8, 9) claims that his *N. Lagerstedti* Cleve (valves by inspection of figures: 15–21 μ l.; 4·5–5 μ br.; str. 16–18 in 10 μ) is the same as *N. ignota*, Krasske having failed to see that the branches of the raphe do

not reach the more apical part of the axial area and that the apical striae consist of two parts. He is probably correct, as these two features are easily overlooked and his diatom is very like Krasske's and mine, apart from the apical striae being radial instead of parallel. On the basis of the structure of the apical striae, Hustedt includes this species with *N. annulata* Grun. (see Schmidt's *Atlas*, pl. 397, figs. 27–29) in a new section, *N. annulatae*, since, according to him, the unstriated part between the apical striae on each side of the valve together form a ring. Unfortunately, apart from the apical valve markings, he gives no description of this species. Hustedt's specimens agree with mine, apart from the radial apical striae and only the more central long ones being weakly curved occasionally (Hustedt, 1937–8 and his figs. 33–37 in Schmidt's *Atlas*, pl. 400) and the extremely regular semicircular form of the unstriated area running across the apical striae.

It is not clear why Hustedt calls his species *N. Lagerstedti* Cleve, since the references he gives (1935, p. 385; 1937–8, p. 254; 1938, p. 360, and Schmidt's *Atlas*, pl. 400, figs. 35–37) all refer to a species *N. Lagerstedtii* Cleve (1894–5, pt. 1, p. 141). Presumably the one *i* is a slip, since there is no *N. Lagerstedti* Cleve but, even then, I am unable to see any connexion between *N. ignota* and Cleve's species. Cleve refers *N. Lagerstedtii* to *Navicula* sp. Lagerstedt (1873, p. 35, pl. 2, fig. 12), and both he and Lagerstedt describe a diatom with indistinct axial and central areas, radial central and parallel apical striae, and Lagerstedt's figure shows three central striae on each side of the valve which are much more prominent than the rest, though barely shorter and not isolated from the rest (str. 12 centrally and 15 in 10 μ apically). The apical striae are not crossed by any line, and the raphe reaches to the end of the striated portion of the valve. The only features in common with *N. ignota* seem to be the triundulate valves, but Hustedt's diatom, like mine and Krasske's, has all the undulations similar and rounded, while Lagerstedt's has the central pair rounded and the more apical pairs pointed. I am, therefore, retaining this diatom in *N. ignota* Krasske.

var. *palustris* Hust. (*N. Lagerstedti* Cleve var. *palustris* Hust. (Hustedt, 1935, 1938 and Schmidt's *Atlas*, *99–100*, pl. 400, figs. 27–29). Fig. 4 Y–CC.

Differs from the species in the shape of the valves (16–21 μ l.; 5–6 μ br.) and in details of striation (density as in species). The larger valves are centrally inflated and have capitate apices. With decrease in size the valves become more linear and less capitate, the smallest (Fig. 4 CC) being completely linear with widely rounded apices. All the striae are radial and curved, except the short central pair. The clear longitudinal lines between the apical striae may be more or less semicircular (Fig. 4 AA, BB) or very irregular due to their fragmentary nature (Fig. 4 Y, Z); sometimes there are three separate portions in a striae. The soil specimens show the same change of valve form with decreasing size as do Hustedt's specimens (Schmidt's *Atlas*, *99–100*, pl. 400, figs. 27–29; Hustedt, 1935, p. 385).

var. *anglica* n.var. Fig. 4 W, X

Differs from the two previous diatoms in the more lanceolate and delicately marked valves which do not become linear with decrease in size as do those of var. *palustris*. The valves (13–16 μ l.; 4–5 μ br.) have weakly subcapitate apices. The relatively thin striae are correspondingly denser (15–20 in 10 μ) and all radial. The shortened central striae number one or two and may be of unequal length.

I have not observed any transitions between the varieties and the species, all three of which occurred on the more alkaline soils (S47; 42, 51 E, var. *palustris*; 20, 21, var. *anglica*). The species is recorded from various more or less aerial habitats in Europe and Asia (Hustedt, 1935, 1938; Krasske, 1932) and var. *palustris* from wet mosses (Hustedt, 1935).

Navicula mesoleiae Cleve

(16) *Navicula seminulum* Grun. (for form variation see Grunow in Van Heurck, 1880–5; Hustedt, 1930; Geitler, 1932; Schmidt's *Atlas*, pl. 401, 1936). Fig. 5 I–GG, II–YY

Valves 4–15 μ l.; 2·5–4 μ br.; str. 20–25 in all but the smallest valves where there may be up to 28–30 in 10 μ.

The valves of the larger cells show considerable variation in form, being linear (Fig. 5 I, Q), elliptic (Fig. 5 AA–CC), lanceolate (Fig. 5 X, Y, EE, FF), or even more or less rhomboidal (Fig. 5 S). There are all intermediate gradations chiefly through the smaller cells, as are shown in the necessarily numerous figures. With decreasing size the valves become elliptic (Fig. 5 I–O), oval (Fig. 5 PP, QQ, TT) or almost spherical (Fig. 5 WW, XX); these latter are all cells of 'minimal size' (Geitler, 1932) and may show rather irregular markings. The apices are always rounded, sometimes broadly so (Fig. 5 P), or very weakly rostrate (Fig. 5 EE, FF). The axial area is always narrow and the central area always wide and more or less rectangular. The branches of the raphe are fine and straight. The striae bounding the transapical margin of the central area are always short and either parallel or, more rarely, in part weakly radial (Fig. 5 CC). Occasionally, especially when somewhat longer than usual, they are curved (Fig. 5 CC). In the larger cells they number three to four and, occasionally, five (Fig. 5 J, Z) on one or both sides of the central area. In the smaller cells there are usually two to three and, very rarely (Fig. 5 UU, XX), one on each side. The last state only occurs in cells of 'minimal size' (cf. Geitler, 1932). There is not the regular diminution of their number seen in Geitler's cultures (1932), but this is probably because a number of different races occur on soil (compare Fig. 5 I, P with CC and Q, J, U and Z). All the other striae are radial and, in the larger cells, often curved (Fig. 5 I, J, Y, AA–CC). While the transition from axial to central area is usually very sharp (e.g. Fig. 5 I–O), sometimes, especially in the larger elliptical cells (Fig. 5 CC), there are one or two striae of intermediate length bounding the central area. In some of the very small valves (Fig. 5 YY) neither the raphe nor more than the marginal portions of the striae could be seen, a feature noted by Geitler (1932, fig. 6*f*) in his cultures.

There would appear to be several races of this species, the smaller cells of which are indistinguishable from one another (e.g. compare Fig. 5 I–O with R, S, X, Y and EE–GG, each group being from a different soil). They commonly occur, however, together in one and the same soil or enriched samples of the same. Geitler (1932, figs. 6, 7) has shown that a certain amount of variation, though not to the degree here shown, occurs in a single clone culture. Further, such cultures are needed to elucidate the status of the various types. The valves of *N. seminulum* are described in Hustedt (1930, p. 272) as linear-elliptic with generally a small median inflation (11–14 μ l.; *circa* 4 μ br.; 18–20 str. in 10 μ), which is also shown in Grunow's figure in Van Heurck (1880–5, pl. 45, fig. 9). Only a few of the very large number of valves I have examined possessed any median inflation (Fig. 5 T, Y, EE, FF), and then hardly to the degree

figured by these workers. Geitler (1932, p. 33 et seq.) also does not record more than a very slight inflation from his cultures and was the first to record the elliptic, oval and subspherical valves. His diatom was originally considered to be *N. minima* var. *atomoides* by Krasske, but later confirmed as *N. seminulum* by Hustedt. Hustedt (1930) and Grunow (1860) also show a valve with almost subcapitate apices, a feature never observed by Geitler or myself. However, in Schmidt's *Atlas* (*101–2*, pl. 401, figs. 50–58), Hustedt figures a variety of valve forms, some broadly elliptical, some linear-elliptical, and some with a slight median inflation, so that he and Geitler together figure all the types shown by me except the large elliptic and rhomboid-elliptic valves. Hustedt (Schmidt's *Atlas*, *101–2*, pl. 401, figs. 59, 60) also figures two of Geitler's small cultural cells which he appears to consider as more or less abnormal ('kummerformen'), though, like Geitler, they appear to me to be merely cells of minimal size and not the product of unfavourable conditions. Since there are all gradations between the various soil forms and most of these have been described by other workers, there do not seem to be any grounds for separating them or for emending the description of the species.

Hustedt's (1937–8, p. 239, pl. 17, figs. 29–33) *N. seminuloides* (valves 5–10 μ l.; 3–3·5 μ br.; str. 20–22 in 10 μ) and its var. *sumatrensis* from Java and Sumatra agree closely with *N. seminulum*, apart from the varying length of the central striae in the larger valves of var. *sumatrensis*. On the basis of Geitler's cultures (1932) he considers *N. seminuloides* differs from *N. seminulum* in that, though the small valves of both are fully elliptic, those of *N. seminulum* arise from and again give rise to, on auxospore formation, large linear individuals. Judging from some of the soil specimens, however, the largest cells, which presumably are the near descendants of the auxospores, may also be rhombic-elliptic or elliptic (e.g. Fig. 5 Y, AA, CC), and it seems to me that *N. seminuloides* can hardly be more than a tropical form of *N. seminulum*. The extreme similarity of the two species is well seen in Hustedt's figures in Schmidt's *Atlas* (*101–2*, pl. 401, figs. 50–60, 68–76).

N. minima Grun. and var. *atomoides* (Grun.) Cleve (see below) show considerable similarity to some cells of *N. seminulum*, but differ in the constantly finer and denser striae (size for size), and the valves of the former species differ from all of those of the latter, except the large linear ones, in the constantly linear shape with widely rounded apices, so that the smallest valves of *N. minima* (Fig. 5 F–H) are oblong as against elliptic, oval or subspherical in *N. seminulum* (Fig. 5 M–O, II, JJ, OO–QQ, TT–YY). *N. minima* also differs from *N. seminulum* in the curvature of the striae in all but the smallest valves, a feature only occurring sporadically in *N. seminulum*, and in the even narrower axial area which passes even more abruptly into the more or less clearly hour-glass-shaped central area, owing to the complete absence of striae of intermediate length. *N. minima* var. *atomoides* (Fig. 5 HH) hardly differs in shape from some of the valves of *N. seminulum* (e.g. Fig. 5 NN), though the same differences in striation are present. Apart from a few of the smallest valves where the markings are particularly difficult to resolve, the two species are clearly distinct under the microscope.

N. seminulum (present on seventeen soils) is a common diatom, mainly on well-cultivated soils where it may be very abundant. It is one of a group of small soil *Navicula* species (e.g. *N. minima* Grun., *N. muralis* Grun. f. *agrestis* f.nov., *N. pseudagrestis* n.sp.) which have probably been confused with one another in the past. Hustedt (1942) records it from damp bryophytes.

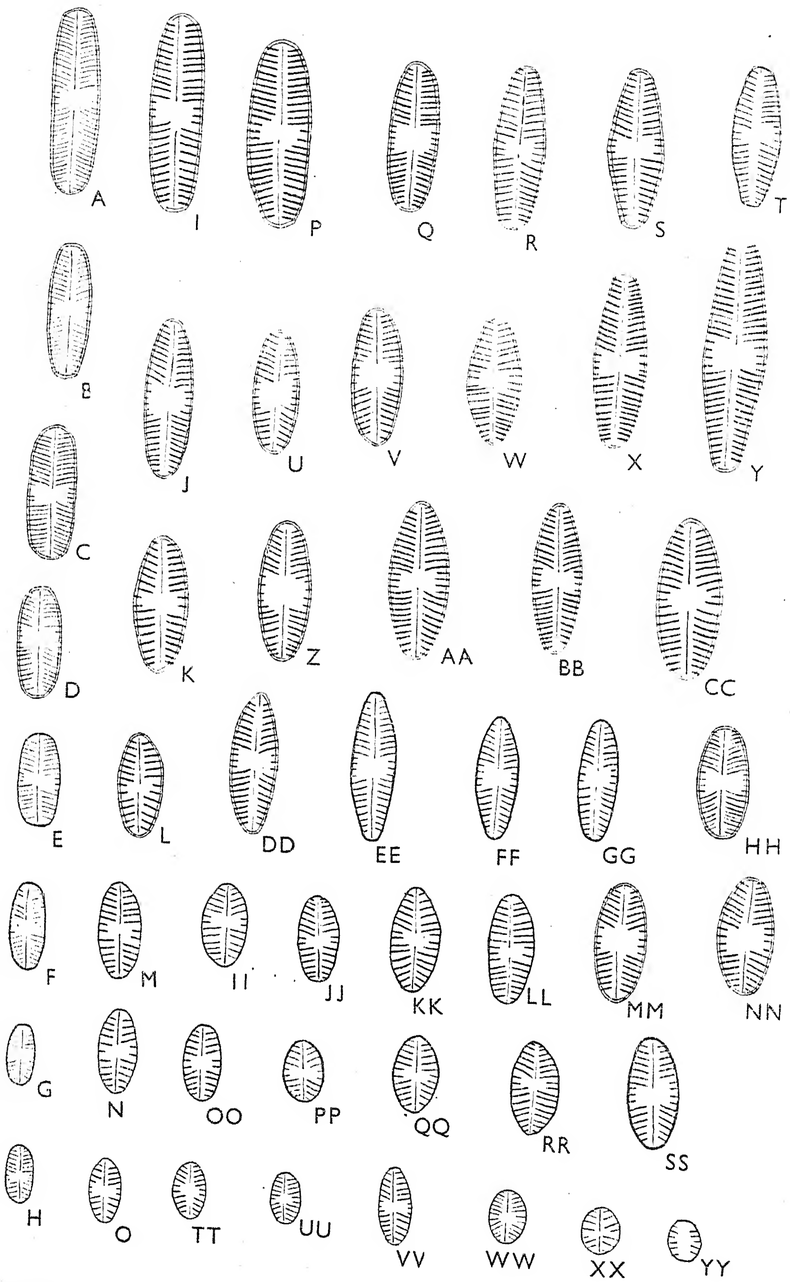

Fig. 5. A–H, *Navicula minima* Grun.; HH, ibid. var. *atomoides* (Grun.) Cleve; I–GG, II–YY, *N. seminulum* Grun. All × 1750.

(17) *Navicula minima* Grun. (? *N. tantula* Hust. forma). Fig. 5 A–H

The valves (4–15 μ l.; 2–4 μ br.) are always linear to linear-elliptic with broadly rounded or slightly flattened (Fig. 5 E) apices. The very narrow axial area passes abruptly into a wide central area. The fine branches of the raphe are straight. The striae (28–30 in the larger and approx. 30–35 in 10 μ in the smaller valves) are all very fine, radial, and, except in the smallest cells, clearly curved, apart from the shortened central ones which are parallel. These latter, two to four in number on each side of the valve, generally stand a little farther apart from one another than do the rest of the striae.

The aquatic forms (Hustedt, 1930, p. 272) differ from the soil specimens in that the central area is scarcely half the width of the valve (often more than half in var. *atomoides*), while, in the soil specimens, it usually reaches to two-thirds the width of the valve and in the absence of curvature of all but the shortened central striae. Hustedt (1937–8, p. 240) notes the similarity of some cells of *N. seminulum* (see also under that species) to this species, but notes that in the Asiatic as in the European specimens the markings of the latter were finer than those of the former.

N. tantula Hustedt (Schmidt's *Atlas*, *99–100*, pl. 399, figs. 54–57; Hustedt, 1935, p. 383) is undescribed, but, from the figures, is similar in shape of valve to the larger valves of the soil form of *N. minima* of which it may be a variety. It has a considerably larger central area than that described for *N. minima*, being even larger than in my specimens. The striae are not curved. By inspection of the figures (Schmidt's *Atlas*, *99–100*, pl. 399, figs. 54–57) the valves measure 8–10 μ l.; 2·5–3 μ br., and there are 29–32 striae in 10 μ.

The longer valves of *N. minima* show some resemblance to *N. densistriata* Hust. (Hustedt, 1930, p. 288, fig. 485), but may be distinguished by the more radial striae and generally greater width in proportion to length.

var. *atomoides* (Grun.) Cleve. Fig. 5 HH

This only differs from the species, so far as the soil specimens are concerned, in the more elliptic valves. Moore & Carter (1926, p. 118) record *N. atomoides* Grun. as the most general of their four soil diatoms. It is also recorded by Moore & Karrer (1919). *N. atemoides* Grun. (presumably the *e* is a slip, as only *N. atomoides* Grun. is known) is referred by Cleve (1894–5, pt. 1, p. 128) to *N. minima* Grun. var. *atomoides* Grun., but may have been confused with *N. seminulum*.

The species, with a few specimens of the variety, occurred on fourteen soils, often with *N. seminulum* and, like that species, appears to favour well-cultivated areas where it may be abundant. Hustedt (1942) records it from bryophytes and McCall (1933) from a porcelain sink in a greenhouse.

(18) *Navicula mutica* Kütz. Fig. 6 A–H

6–30 μ l.; 4–8 μ br.; str. 18–24–27 (smallest cells) in 10 μ.

Numerous forms and varieties have been described (cf. Petersen, 1928, p. 389; Hustedt, 1937–8, p. 231 et seq.), but, following Hustedt's classification (1930, p. 275), I have observed vars. *ventricosa* (Kütz.) Cleve, var. *nivalis* (Ehr.), var. *binodis* Hust. and, most commonly, var. *Cohnii* (Hilse) Grun., together with various intermediate forms, all of which occurred with the species though any one soil tended to be dominated by one particular form. There can be little doubt that the end members of the growth series of the capitate and rostrate forms come near to the species and var. *Cohnii*, the

valve form being simplified with the decrease in size. The larger valves are, however, quite distinct from the species.

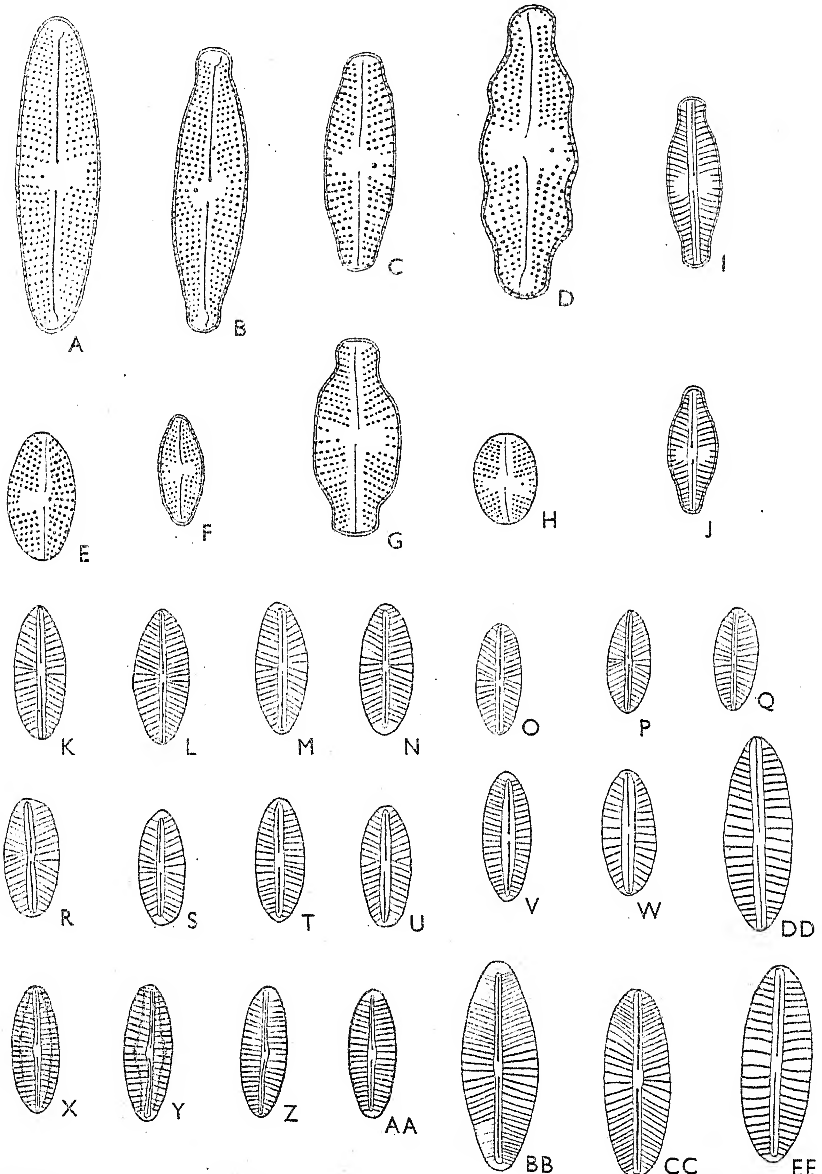

Fig. 6. A–H, *Navicula mutica* Kütz.; D, var. *nivalis* (Ehr.) Hust.; E, H, var. *Cohnii* (Hilse) Grun.; I, J, *N. Heufleriana* (Grun.) Cleve var. *minor* n.var.; K–W, *N. pseudatomus* n.sp.; X–AA, *N. pseudagrestis* n.sp.; BB, CC, *N. Vaucheriae* Boye Pet. var. *densistriata* n.var.; DD, EE, *N. Vaucheriae* Boye Pet. All ×1750.

This is one of the commonest of all soil diatoms (present on thirty-eight samples) on soils which are not base-deficient, especially those containing appreciable amounts of calcium carbonate where it may occur in quantity. It is one of the few diatoms occurring on such soils which are also deficient in nitrates and available phosphate (e.g. S 8, 26, 55, 56).

John (1942) records it as typical of calcareous soils and Hustedt (1937–8, p. 234) in various neutral to alkaline waters.

(19) *Navicula Heufleriana* (Grun.) Cleve var. *minor* n.var. Fig. 6 I, J

The elliptical valves (9–13 μ l.; 4–5 μ br.) are centrally inflated and decrease sharply in width towards the rostrate to weakly capitate apices. To each side of the raphe there lies a clearly marked area which appears similar to that in *N. pseudatomus* n.sp. and *N. Vaucheriae* Boye Pet. (q.v.). This occupies the whole of the axial area, but the central area extends beyond it and is rectangular to oblong. The striae (23–28 in 10 μ) are radial, curved and faintly punctate.

This diatom resembles *N. Heufleriana* (Grun.) Cleve in the shape of the valves, apart from the less markedly capitate apices, in the radial, finely punctate dense striae, the narrow axial and wide rectangular area. *N. Heufleriana* is, however, much larger (valves 24–32 μ l.; 8–9 μ br.) with coarser striae and is considered to be closely similar to *N. mutica* var. *ventricosa* (see above) by Cleve (1894–5, pt. 1), while Hustedt (1930, p. 274) thinks that it belongs to this diatom. My variety is unlike *N. mutica*, apart from the shape and the radial though finely punctate striae. Grunow (in Hustedt, 1930, fig. 452) demarcates the axial area by a thick line, suggesting that, though it is not mentioned, he may have observed something similar to that seen in this variety. On the other hand, Hustedt (1924, p. 556, pl. 17, fig. 4) neither mentions nor figures any such demarcation of the axial area in his var. *septentrionale*. The valves (15 μ l.; 3·5 μ br.) of this variety are less inflated than in the species, and the striae (20–21 in 10 μ, by inspection) are relatively thick but not clearly punctate judging from the figure.

N. ventralis Krasske (Hustedt in Schmidt's *Atlas*, pl. 400, figs. 73–77; 1942, p. 70, fig. 17) has valves of similar shape but generally much more convex and capitate, while there is no clear demarcation of the axial and central areas.

Present in an enriched sample from an allotment soil (S 44).

(20) *Navicula Brockmanii* Hust. (?*N. bryophila* Boye Pet.). Fig. 4 M, N

Valves (13–15 μ l.; 3–4 μ br.) linear centrally with cuneate apices. Branches of the raphe straight. Axial area very narrow, central area oval to elliptical and small. The more central striae (25–30 in 10 μ) are radial and often curved. The denser (35–40 in 10 μ) very fine apical striae are parallel or very weakly convergent.

The soil specimens differ from those from mosses (Hustedt, 1935, p. 382, fig. 11; 1942, p. 63) in the smaller size (17 μ l.; 4·5 μ br.; 30 str. in 10 μ), the slight convergence of the most apical striae, and the apparent absence of curvature of the slits of the polar nodules. The last feature may be present, as it was extremely difficult to observe the apical portions of the raphe.

In the shape and fine striation this species shows some resemblance to *N. bryophila* Petersen (1928; Hustedt, 1937–8, p. 248, pl. 18, figs. 18–23), another aerial species, but differs in the orientation of the more apical striae.*

Observed in an enriched sample of one soil (S 47).

Navicula entoliae Cleve

(21) *Navicula contenta* Grun. Fig. 13 L, M

7–19 μ l.; 2–3 μ br.; approx. 35 str. in 10 μ. The species and f. *biceps* Arnott and

* Hustedt's accounts and figures cited above are at variance with his figures in Schmidt's *Atlas* (Pl. 404, figs. 40–48, 1936) where the apical striae are clearly convergent.

parallela Boye Pet. occurred in small numbers on eighteen soils. Bristol (1920, p. 70) obtained specimens in cultures of fourteen soils which had been subjected to desiccation. Petersen (1928, p. 395) states that it is specially common on rocks, and Krasske (1932) found it as a typical inhabitant of xerophytic mosses (cf. Beger, 1928). I have also found it in tufts of diverse mosses. West, W. & West, G. S. (1899) found specimens on the leaves of trees in Dominica which presumably would be dry at times. It seems, therefore, that it grows best under strongly xerophytic conditions of an aerial rather than terrestrial nature. It is also likely that it can flourish where nutrients are particularly scarce.

Navicula bacillares Cleve

(22) *Navicula pseudatomus* n.sp. (? *Synedra atomus* Kützing (1849); ? *Navicula atomus* Naegeli (1849); ? *N. atomus* (Naeg.) Grunow (1860); probably *N. atomus* (Naeg.) Grun. in Van Heurck (1880–5, 1899); *N. atomus* (Naeg.) Grun. in Petersen (1915, 1928, 1935), Bristol (1920); non *N. atomus* (Naeg.) Grun. in Hustedt, 1930; ? *N. caduca* Hustedt (1942)). Fig. 6 K–W.

The taxonomy of this common soil diatom is very confusing. Hustedt's description and figure (1930, p. 287, fig. 484) do not mention or show the prominent, thickened axial area characteristic of the species, the variable length and orientation of the central striae, the common occurrence of feebly silicified cells and the relatively robust raphe, and are at variance with those of Van Heurck (1880–5, p. 107, pl. 14, figs. 24, 25, drawn by Grunow; 1899, p. 227, pl. 5, fig. 231), who describes it as 'feebly silicified' with a robust raphe; of Cleve (1894–5, pt. 2, p. 4), who refers to the figure in Van Heurck (1880–5) and to that of Grunow (1860) without, apparently, realizing the difference between them (see below). Cleve describes the cells as 'slightly silicious'. Petersen (1915, p. 289, fig. 11; 1928, p. 387) describes it as 'extremely delicate' with 'the raphe surrounded by a clear hyaline zone', and Bristol (1920, p. 70, text-fig. 9, figs. 9, 11–13) describes the cells as 'extremely hyaline' and 'most strongly silicified around the raphe'.

Naegeli (1849) refers it to Kützing's *Synedra atomus* (as does Cleve, 1894–5), but neither Kützing's (1849, p. 40, no figures) nor Grunow's descriptions (1860, p. 552, pl. 2, fig. 6) elucidate the position. Grunow's figure shows the narrow axial area and unclear central area of Hustedt's (1930) species but does not show the markedly radial striae. It is so nebulous as to make it doubtful as to what species is figured. On the other hand, his figures in Van Heurck (1880–5, pl. 14, figs. 24, 25; he also assisted in the preparation of the text of this work) do show a wide convex area around the raphe, relative to that shown by Hustedt (1930), both figures being drawn to the same magnification. However, here again (and in Van Heurck, 1899, pl. 5, fig. 231) the figure is not clear enough to be certain that this is the *N. atomus* of workers on soil diatoms. Further, the density of the striae of all these earlier workers, and of Hustedt, is greater than those given by soil workers. In view of the difference of Grunow's own figures and the uncertainty of the identity of the soil and aquatic specimens, it is necessary to make this a separate species. There seems little doubt that Hustedt's *N. atomus* is not that of Naegeli or Grunow and should be renamed.

Hustedt (1942, p. 64) states that Petersen's fig. 11 (1915) cannot be *N. atomus* (sensu Hustedt), in that it shows about 20 striae in 10 μ. He considers it belongs to the closely allied group of *N. asellus* Weinhold, *N. spirans* Hust., *N. excelsa* Krasske and *N. caduca* Hust. While it is not clear as to which of these it does belong, he favours *N. caduca*

(Hustedt, 1942, fig. 4, 5 μ br.; 10 μ l.; 19 str. in 10 μ; from mosses) which has a sharply demarcated axial area, very strongly radial striae, somewhat denser centrally than apically, apical nodules some distance from apex of the hyaline and thin valve. He does not mention any weak silicification of the valve or the presence of a thickened axial area, though its prominence suggests that this may be the case. There are also shortened striae to each side of those opposite the central nodule, a feature never seen in *N. pseudatomus*. It remains doubtful, therefore, whether *N. caduca* belongs here or not.

Petersen (1935) has rightly pointed out that Bristol's (1920) text-fig. 9, fig. 10, cannot belong here, since it is very narrow in girdle view.

I have examined a very large number of specimens, all of which agree in having very thin frustules, elliptical valves, radial striae and a clearly differentiated hyaline area around the straight branches of the raphe and the central nodule. The valve is generally weakly silicified and often, after cleaning with acid, only the axial area remains. This is similar to that in *N. Vaucheriae* Boye Pet. (Petersen, 1935, and see below), where the raphe is said to lie in a silicious rib, and the greater resistance of the axial area of *N. pseudatomus* suggests that its raphe is similarly enclosed. The axial area is sometimes constricted centrally (Fig. 6 R) and it varies considerably in width (Fig. 6 L–N, U–W). The valve size (6–10 μ l.; 2–5 μ br.) may be somewhat greater than recorded for *N. atomus* (Van Heurck, 1880–5, 1899; Cleve, 1894–5, and Hustedt, 1930, 4–8 μ l.; 2–5 μ br.). I have not observed any of the larger specimens of Petersen (1915, 1928) and Fritsch & John (1942) which reached 14 μ l. and 7 μ br. These may belong to *N. Vaucheriae* var. *densistriata* n.var. (p. 76). Bristol's (1920, p. 70) valves measured 9–11 μ l., and 4–5 μ br. There were 18–20 striae centrally and about 26 in 10 μ apically. Their density was usually greater in the cells with relatively narrow axial areas (Fig. 6 L–N) than in those with wide axial areas (Fig. 6 T–W). The latter were thus similar to the larger *N. Vaucheriae* (Fig. 6 DD, EE). One or two central striae are often perpendicular (Fig. 6 K, L) and may be much shortened as well, in which case they may bisect the angle made by the striae to each side of them (Fig. 6 P, R), or one of the two central striae forming a central V is shorter than the other (Fig. 6 U). The central striae are generally more delicate than the rest.

Next to *Hantzschia amphioxus* this is the most ubiquitous soil diatom, often occurring in great abundance on well-cultivated soils (see Part 1, D2 for its ecology). The forty-four soils on which it occurred ranged from *p*H 4·4 to 8·3.

(23) *Navicula Vaucheriae* Boye Pet. (Petersen, 1915, emend. 1935, p. 145). Fig. 6 DD, EE

The British specimens are mostly larger than the one on which Petersen founded the species. The axial and central areas of the elliptical valves (10–15 μ l.; 5–6 μ br.) differ strongly in appearance from the rest of the valve. Petersen states that this is due to the raphe being enclosed between siliceous ribs, but it would seem to me to be rather due to a generalized thickening of the valve in that region. Sometimes there is a small indentation on one side of the central area (Fig. 6 DD; cf. Petersen, 1935, fig. 5). The striae are somewhat radial, occasionally curved (Fig. 6 EE), the central ones (about 16 in 10 μ) standing farther apart than those near to the apices (about 20–25 in 10 μ).

This diatom is allied to the usually clearly smaller *N. pseudatomus*, from which it differs in the less dense, less radial striae, of which the central ones are as prominent as the rest and never shortened. Petersen (1935) states that it is hardly possible to

distinguish the small specimens of this species from specimens of *N. pseudatomus* (*N. atomus* in his account) and *N. muralis* Grun. I have usually found the distinction quite clear, though some specimens of *N. pseudatomus* (Fig. 6 V, W) show similar striation. Krasske's *N. insociabilis* (see p. 77) is said by him and Petersen (1935) to differ from this species in the coarser, definitely punctate or transversely striate striae. Hustedt (1942, p. 68, fig. 5) refers to the similarity between his *N. minusculoides* and Petersen's (1915, fig. 13) original figure of this species which showed parallel striae, but apart from Petersen's emendation (1935) of this description, *N. minusculoides* has denser striae (26 in 10 μ).

This uncommon diatom, only recorded from soils, occurred on three woodland samples (S8, 20, E).

var. *densistriata* n.var. (Fig. 6 BB, CC)

Valves (14–16 μ l.; 5–6 μ br.) very delicate and weakly silicified, broadly elliptical with rounded apices. Branches of the raphe straight and enclosed in a narrow thickened area which has a small inflation on one side opposite the central nodule. Striae (approx. 18–20 centrally and 30–35 apically in 10 μ) all radial except the one or two to each side of the central nodule; the more central much less dense and somewhat thicker than the more apical ones but none of them prominent.

Differs from the species in the finer striation (especially apically) and greater difference in density between the central and apical striae. No transitional forms have been seen. *N. excelsa* Krasske (Hustedt, 1930, p. 307; also in Schmidt's *Atlas*, *99–100*, pl. 400, figs. 60–68) is similar in appearance but differs in the coarser striation, wider more lanceolate axial area and apparent absence of a centrally thickened area of the valve. For relationship to large specimens of *N. pseudatomus* see p. 75.

A few cells occurred on three soils (S29, 37, 47).

(24) *Navicula pseudagrestis* n.sp. Fig. 6 X–AA.

The elliptical valves (9–11 μ l.; 3·5–4 μ br.) are widely rounded apically. The raphe is enclosed in a thickening of the valve ('silica rod'), one side of which is convex centrally as in the preceding diatom and *N. Fritschii* n.sp. (p. 77) and is sometimes rather excentric (Fig. 6 Y). The striae (23–28 in 10 μ) are all straight and radial, except in the centre where they are almost parallel. The portion of each stria nearest the valve margin is more prominent and thicker than that near the axial area. At the junction between the two parts there is often a clear or faint line running along the length of the valve. This line, which may be in the form of a regular curve (Fig. 6 X) or arched centrally (Fig. 6 Y), cannot be demarcated sharply and appears to be due to a depression in the valve face.

This species is similar to Hustedt's specimens said to be of *N. insociabilis* Krasske (styrax mounts) described on p. 77. It differs only in the central one-sided inflation on the siliceous thickening surrounding the raphe, the varying thickness of the outer and inner parts of the striae and their greater density. From Krasske's original description of *N. insociabilis*, it differs in these features and in the longitudinal line crossing the striae.

It seems probable that this is the same as Bristol's (1920, p. 68, text-fig. 19, figs. 18–21) *N.* (sect. *Diploneis*) *hyalina* Donk. var. *minima*, whose striations (27–37 in 10 μ) were

only clear near the margin of a valve possessing a similar longitudinal furrow in the same position and whose raphe lay in a clearly differentiated area which Bristol considered to be a furrow. The valve (11–14 μ l.; 3·5–4·5 μ br.) was also elliptic.

Though this diatom occurred in enriched samples from six soils, it was only observed in one by direct examination (S 5) but then in considerable numbers. The name refers to its resemblance in shape and size to *N. agrestis* Hustedt (1937–8, p. 246).

(25) *Navicula Fritschii* n.sp. (*N. insociabilis* (Krasske) Hustedt pro parte in Hustedt, 1937–8). Fig. 7 A–G

The valves (7–16 μ l.; 5–6 μ br.) of the larger cells (Fig. 7 A–C) are elliptic to ovate-elliptic with widely rounded apices. With decreasing size (Fig. 7 D–G), the valves become more and more oval. The largest valves may be weakly inflated centrally (Fig. 7 A), being usually more convex on one side than on the other (cf. Hustedt's fig. 26 in Schmidt's *Atlas*, *99–100*, pl. 400, 1934). The raphe is straight except near the central nodule, where each branch bends more or less clearly towards one side of the valve (Fig. 7 B, C). The polar slits can be seen in the larger valves to be hemispherical. Neither branch reaches the end of the valve, for the whole of the raphe is enclosed in a more strongly silicified portion of the valve. This siliceous 'rod' is wider near the central than the polar nodules and is markedly convex opposite the central nodule on that side towards which the branches of the raphe may bend. On one or both sides of this rod lie a row of very short striae, which are often difficult to resolve and appear to be absent over part of its length at times (Fig. 7 A, B, F). They never occur opposite the central nodule (cf. Hustedt, Schmidt's *Atlas*, pl. 400, figs. 19–26). Between these and the more marginal striae (20–25 in 10 μ) there is a wide lanceolate area devoid of markings, while another narrower line free of markings divides the more marginal striae into two parts.

The taxonomy of this diatom is very confusing. Hustedt (1937–8, p. 252) states that it is identical with *N. insociabilis* Krasske (1932, p. 114, pl. 3, fig. 17). This diatom appears closely similar to *N. Vaucheriae* Boye Pet. (see p. 75), though Petersen (1935), who has seen Krasske's specimens, agrees with him that it is a distinct species, characterized by the coarser lineate striae. The valves (12–18 μ l.; 5–7 μ br.) of *N. insociabilis*, as described by Krasske, are elliptic with rounded apices and do not have any central inflation. The axial area is very slightly lanceolately widened opposite the central nodule, and the raphe lies in a siliceous thickening. The striae (20 in 10 μ) are radial and not crossed by any longitudinal lines. It is recorded from mosses. Hustedt has figured two apparently different diatoms in Schmidt's *Atlas* (pl. 400, 1934), one from hyrax (figs. 19–26), the other from styrax (figs. 104, 105) preparations. The former agrees with *N. Fritschii* in size (valves 16–21 μ l.; 5·5–6 μ br.; approx. 22 str. in 10 μ, measurements by inspection of Hustedt's figures) and structure. The latter, from styrax mounts, is similar in size of valve (10–11 μ l.; 4·5–5 μ br.; approx. 21–23 str. in 10 μ, by inspection of figs. 104, 105) to the smaller ones of *N. Fritschii* but differs strongly in appearance. It is like Krasske's description of *N. insociabilis*, apart from a longitudinal line crossing the striae and lying about half-way between the centre and margin of the valve. Hustedt (1937–8, p. 252) states that it is the difference in mountants used by him and Krasske that makes the two diatoms look so unlike and that the small styrax specimens, when mounted in hyrax, look completely different and the same as the larger specimens. In spite of Hustedt's statement, I am of the opinion that there are two distinct species.

It seems most remarkable that mounting in the less refractive styrax results in the loss of the characteristic shape of the siliceous 'rod' (compare Hustedt's figs. 25 and 105 in Schmidt's *Atlas*, pl. 400), makes the branches of the raphe appear straight or almost so, and makes it appear that the striae cover the wide area free of striation to each side of the siliceous 'rod', as seen in hyrax preparations. In my specimens of *N. Fritschii*, mounted in hyrax and the antimony bromide-piperine mixture, the valve markings are much more prominent than in most soil diatoms of the same size. Further, *N. pseudagrestis* n.sp. (see p. 76) shows a structure closely similar to that seen in Hustedt's styrax preparations of *N. insociabilis*, though mounted by me in hyrax or antimony bromide-piperine mixture and in company with *N. Fritschii*, which here shows the structure described by Hustedt for *N. insociabilis* when mounted in hyrax. Here we have the two types of markings seen in the same preparation.

N. (*Diploneis*) *hyalina* Donk. var. *minima* Bristol (1920, p. 68) may possibly belong here but more probably to *N. pseudagrestis* n.sp. (p. 76), though the extreme delicacy of her specimens makes it impossible to be certain. Petersen (1935, p. 142) suggests that Bristol's diatom belongs to *Frustulia vitrea* Østr. (*Navicula festiva* Krasske and *N. vitrea* (Østr.) Hust.; see Petersen, 1932*a*), recorded from mosses and damp soil, but the latter differs from the former in the bluntly rostrate apices. Petersen's (fig. 3, 1932) and Bristol's (1920, text-fig. 9, figs. 18–21) diatoms appear to possess a similar kind of area free of markings around the raphe to *N. Fritschii* and a siliceous 'rod' around the raphe, but this does not seem to be the case with Hustedt's *N. vitrea* (Østr.). *N. Fritschii* is clearly distinct from *Frustulia vitrea* sensu Petersen and sensu Hustedt, in that the striae are definitely composed of more than one part, reach to the margin of the axial area and are coarser.

Hustedt's *N. vitrea* (Østr.) is clearly distinct from his figures (1930, fig. 489; Schmidt's *Atlas*, pl. 404, figs. 56–58, 1936).

N. Fritschii shows certain similarities to species of *Diploneis* and, especially, *Caloneis*. While the longitudinal lines in the latter are generally not due to actual breaks in the transapical striation, Cleve (1894–5), in his original description of the genus, states that the lines may be due to broad lateral areas and *C. Zachariasi* Reichelt (Hustedt, 1930, p. 234, fig. 355) shows similar striation to *N. Fritschii* without the characteristic siliceous 'rod' enclosing the raphe. *Navicula sejuncta* A. Schmidt (Hustedt, 1930) has the branches of the raphe enclosed but after the manner of a *Diploneis* (cf. Schmidt's *Atlas*, pl. 7, fig. 50; pl. 212, figs. 9, 10).

N. Fritschii was present on seven soils, none of which was base-deficient and all contained appreciable amounts of calcium carbonate.

(26) *Navicula fossalis* Krasske. Fig. 7 H–K

The diatom described here appears to belong to this species though there is a possible difference in the axial area (*vide infra*), for which reason I have placed it in this section of the genus. The elliptic valves (10–12 μ l.; 4–5 μ br.) have an axial area which is narrow near the apices but widens gradually towards the centre, so that there is no definite central area. The straight branches of the raphe and the central nodule are flanked on each side by a faint narrow area, which is lighter than the rest of the valve (indicated by dotted lines in the figures). The striae are radial, the central (approx. 15 in 10 μ) being less dense than those near the apices (approx. 18–20 in 10 μ), and

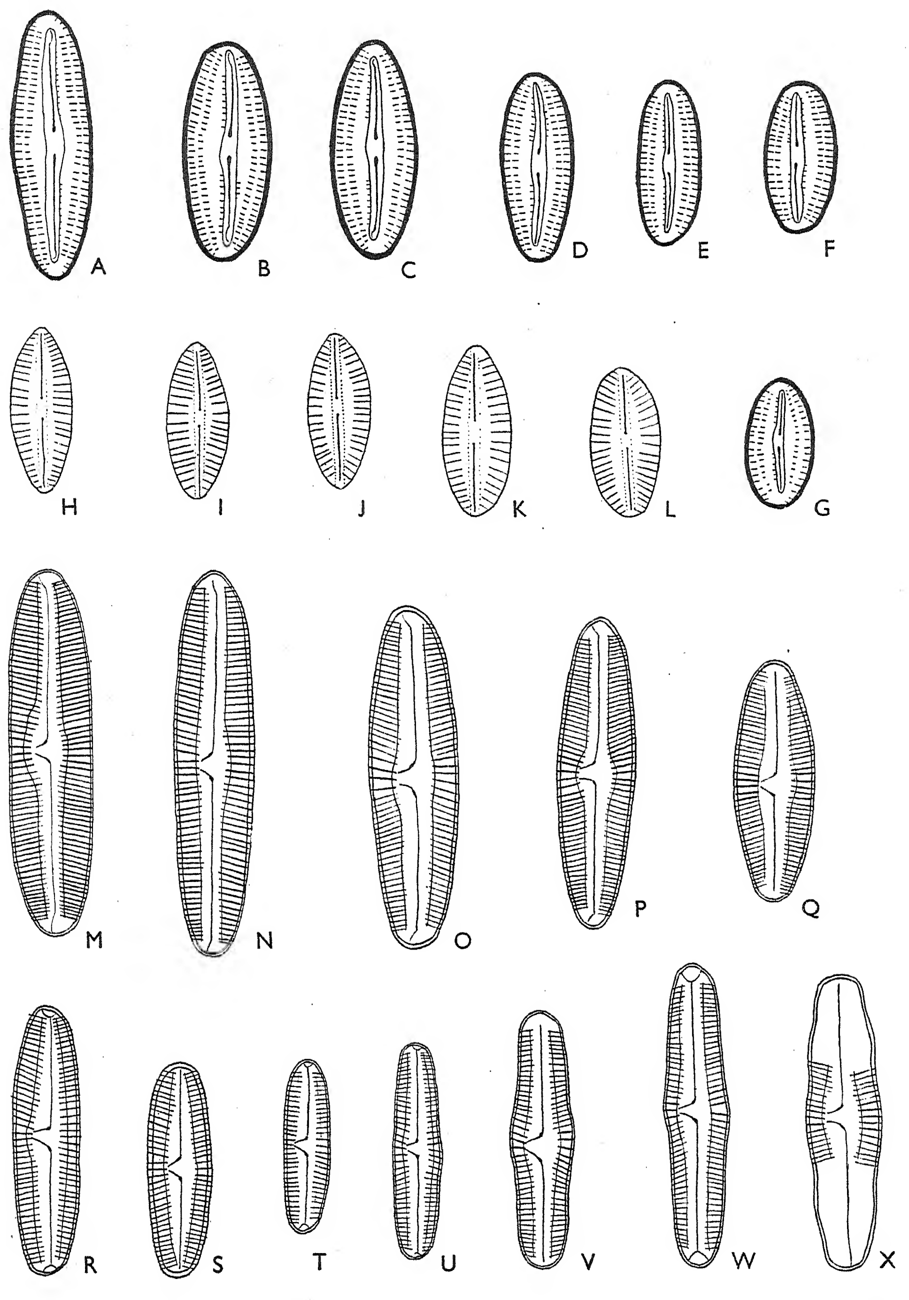

Fig. 7. A–G, *Navicula Fritschii* n.sp.; H–L, *N. fossalis* Krasske; M–T, *N. terrestris* Boye Pet.; U–W, ibid. var. *relicta* (McCall); X, ibid. f. *triundulata* n.f., apical striae not shown. All × 1750.

only the latter reach the hyaline area enclosing the axial area. This area may represent a similar thickening of the valve to that in *N. Vaucheriae*, *N. pseudatomus*, etc. (q.v.), and is not described for Krasske's specimens. *N. subfossalis* Hust. (Hustedt, 1935, p. 383, figs. 14, 15) possesses such a thickening and is of similar size (valves 9–11 μ l.; 3·5–4·5 μ

br.; str. 20–22 in 10μ) but differs in the well-defined central area produced by the shortened striae opposite the central nodule. Hustedt (1942, pp. 66–7, figs. 18, 19) records a more marked distinction between central and axial area for *N. fossalis* than does Krasske (or in Hustedt, 1930, p. 307, fig. 544). The larger and coarser *N. confervacea* Kütz. would appear to be closely related to this species though placed by Hustedt (1930, p. 278) in the section *entoliae*.

Observed once on a woodland path (S17), previously recorded from *Sphagnum* in a woodland ditch and from mosses (Hustedt, 1930, 1942).

Navicula fistulatae McCall (1933)

(27) *Navicula terrestris* Petersen, 1915 (? *N. gibberula* Lagerstedt, 1873; non *N. gibbula* Cleve, 1894–5; *N. gibbula* Cleve in Østrup, 1910; *N. terricola* Bristol, 1920; *N. gibbula* Cleve in Bachmann, 1921; *N. gibbula* Cleve in Hustedt, 1924, 1930, 1935; *N. gibbula* Cleve and *N. relicta* n.sp. in McCall, 1933; *N. gibbula* Cleve var. *terrestris* n.var. in Petersen, 1935). Fig. 7 M–X

The taxonomy of this species is very confusing, and it seems probable that two separate species have been described under *N. gibbula* Cleve. All the descriptions of the valves agree in:

(i) Linear-elliptic shape.

(ii) The fairly wide linear axial area widening somewhat into an oval-elliptic central area.

(iii) The radial punctate striae which are more prominent and less dense near the centre than near the apex of the valve.

Varieties occur having medianly inflated, capitate and undulate valves with or without parallel to weakly convergent apical striae. The soil specimens also differ from the others in their smaller size and correspondingly finer markings.

The points at which the descriptions are at variance are:

(i) The shape of the valve apex.

(ii) The occurrence of a longitudinal line crossing the striae close to the axial area.

(iii) The occurrence of a siliceous thickening (rod) enclosing the branches of the raphe.

(iv) The occurrence of slit-shaped processes arising at the point where the raphe branches pass into the central nodule, both of which bend towards the same side of the valve.

Lagerstedt's *N. gibberula* 'Kütz.' (1873, p. 30, pl. 1, fig. 7) is not clearly described. In fig. 7*a* he shows a centrally inflated valve with a fine longitudinal line crossing the striae in the region near and opposite the central nodule but not reaching the apical portions of the valve. This line lies close to the axial area. He shows two more such lines close to the margin of the valve which run parallel to one another and across all the striae. He does not show any slit-shaped processes at the central nodule. He does not refer to any longitudinal lines in the text, his 'lineis duabus subrectis' evidently referring to the margins of the axial area (cf. his descriptions of *N. bisulcata*, *N. polaris* *N. parvula*, etc., in the same paper). *N. gibberula* Kütz. is, moreover, not a valid name, as it refers to a quite different diatom (*Caloneis silicula* Ehr. var. *gibberula* (Kütz.) Grun.; Cleve, 1894–5, pt. 1, p. 51; Hustedt, 1930, p. 238).

Cleve (1894–5, pt. 1, p. 140, pl. 5, fig. 17) refers his *N. gibbula* to Lagerstedt's *N. gibberula*. It, too, does not show any slit-shaped processes at the central nodule.

In addition, there are no longitudinal lines crossing the striae and the apices are truncate. Østrup (1910, pp. 235–6, pl. 14, fig. 2) records *N. gibbula* Cleve and his figure of var. *capitata* Lagerst. (*N. gibberula* var. *capitata* Lagerstedt, 1873, pl. 1, fig. 7*a*) agrees in valve markings with *N. gibbula* Cleve (1894–5), apart from the parallel striation near the apices. Bachmann and Lötscher (in Bachmann, 1921, p. 36, fig. 10*a*) also record this variety and refer to Østrup's account but state that there is a fine longitudinal line running across the punctate striae, close to the margin of the axial area. All these authors record the species and variety from arctic regions (Spitzbergen, Beer's Island, Greenland).

Hustedt (1924, pp. 558–9, fig. 8) recorded *N. gibbula* Cleve from Swedish Lapland and considered it to be a glacial relict (see above). Further, he examined Bachmann and Lötscher's (1921) specimen of var. *capitata* Lagerstedt and pointed out that, unlike those of Cleve (1894–5) and Østrup (1910), this and his own specimens agree in having a longitudinal line running parallel to the axial area, the raphe lying in a more strongly thickened portion of the membrane and the central nodule drawn out into two slit-shaped processes, both bending towards the same side of the valve and running into the striated portion thereof. Further, in girdle view, the cell was sometimes weakly concave centrally. He considered that these features were really present in Cleve's and Østrup's specimens, and that Lagerstedt wished to indicate the longitudinal line in his *N. gibberula* 'Kütz.' McCall (1933, p. 247) is, however, in error in stating that Hustedt has seen the original specimens of *N. gibbula* Cleve, and it seems remarkable that so experienced a worker as Cleve should not only have overlooked the longitudinal line, which is often faint, but also the marked processes from the central nodule which are so characteristic of the species (cf. McCall's photograph, 1933, fig. 14*b*). In addition, Cleve's species possesses truncate apices unlike those of any figured by all other authors or any observed by me on soils. Lastly, his central area is more oval and more sharply circumscribed than is usual. I am, therefore, of the opinion that Cleve's *N. gibbula* cannot be considered the same as Hustedt's (1924 and see also 1930, p. 285, fig. 477), while Lagerstedt's (1873) description is not clear enough for any determination to be made.

In 1915 (p. 285, figs. 7, 8) Petersen described *N. terrestris* from Danish soils. In the shape of both valve and girdle view and in the valve markings, apart from the absence of the longitudinal line and the thickening of the valve membrane around the raphe, it agreed with *N. gibbula* Cleve sensu Hustedt. Hustedt (1930, p. 285) stated that *N. terrestris* did belong to *N. gibbula*, but Petersen (1935, p. 144) later made it a variety (*terrestris*), differing from the species in its smaller size and finer striation, both of which, however, are untrustworthy features on which to separate soil from aquatic specimens of the same species. It is clear, therefore, that his original *N. terrestris* did actually agree in all significant respects with *N. gibbula* Cleve sensu Hustedt, and since Hustedt's diatom can hardly be that of Cleve and Petersen's has priority over any other valid name, I have retained this diatom in *N. terrestris* Boye Pet.

Petersen (1935, p. 144) stated that *N. terricola* Bristol (1920, p. 67, text-fig. 8, figs. 15–17) might belong here. That this is the case there can be no doubt. *N. terricola* agrees in the possession of a longitudinal line across the striae, often appearing as a row of dots (cf. Bristol's fig. 15), the hyaline nature of the valve around the raphe (the local thickening of Hustedt) and the slit-shaped processes from the central nodule (considered

as part of a sigmoid raphe by Bristol). Bristol's description and figures are not, however, altogether clear or consistent. The slit-shaped processes are not shown in one figure (16). Unlike all the workers, except Østrup (1910), she describes the striae as being almost parallel near the central nodule and weakly convergent near the apices, but in her figures they are all radial. McCall's (1933, p. 248, fig. 15 *a*) *N. relicta* has parallel to weakly convergent apical striae and the median inflation of the valve margin shown by Bristol. This is a variety of *N. terrestris* (var. *relicta*; see below).

Bachmann (1921) suggested that the longitudinal line pointed to this species belonging to *Caloneis* or a new genus. Hustedt, however, states (1924, p. 558) that it is not comparable to the type of line in *Caloneis* and, at the most, the species might be placed in a new subgroup of *Navicula*. McCall (1933) has made a new section, *fistulatae*, for it (and *N. relicta* McCall), though Hustedt (1930) placed it in the *decipientes*. In view of its markings, which are unlike those of any other *Navicula* sp., I follow McCall.

The valve markings have been figured in diverse ways. These differences depend on whether one interprets them as poroids lying between ribs (of which the longitudinal line is a specially prominent member) or as punctate striae, and whether the striations or punctae are shown as black areas or are left as clear areas between the remaining black portions of the valve. Thus, Hustedt's fig. 8 (1924) and McCall's figs. 14 *a*, 15 *a* (1933) produce the appearance of a lattice work, while Hustedt's fig. 477 (1930) and Petersen's fig. 7 (1915) show ordinary punctate striae (see also McCall's photograph, 1933, fig. 14 *b*). Bristol's figs. 15, 16 (1920) show unbroken striae as do mine. In my case, this is due to the fact that, though the striae are clearly punctate, the punctae are not sharply enough defined to enable me to represent them all separately with equal accuracy.

McCall's (1933) *N. relicta* differs from *N. terrestris* Boye Pet. (*N. gibbula* Cleve in McCall's account) in the linear valves which may be slightly gibbous centrally in the coarser 'longitudinal ribs' and the parallel striations near the apices. He notes that it may be Lagerstedt's (1873) *N. gibberula* var. *oblonga*, but this is not gibbous centrally though var. *capitata* Lagerstedt (1873) is. Though Hustedt (1930) does not mention the occasional gibbosity of the valve, Petersen (1915) and Bristol (1920) do, and I have found this type as a common variety, almost always occurring with the species and, as in McCall's species, the gibbosity usually goes with smaller size and somewhat convergent or parallel apical striae. The valves may be linear to linear-elliptic, quite apart from the presence of a central gibbosity (e.g. Petersen, 1915, fig. 7; Bristol, 1920, fig. 16; Hustedt, 1930, fig. 477 and my Fig. 7 M, N). There do not, therefore, seem to be any grounds for making this a separate species.

The previously recorded dimensions for *N. terrestris* Boye Pet. (*N. gibbula* Cleve sensu Hustedt, etc.) are:

(i) Aquatic or semi-aquatic habitats, 20–45 μ l.; 6–10 μ br.; str. 13–16 centrally and up to 22 apically in 10 μ.

(ii) Terrestrial habitats, 15–37 μ l.; 4·5–8·5 μ br.; str. 18 centrally, 25 apically in 10 μ.

The soil specimens I have observed show even wider variation than heretofore described.

N. terrestris Boye Pet. Valves (13–33 μ l.; 4–7 μ br.) linear-elliptic or elliptic (Fig. 7 Q). Apices widely rounded. Axial area narrow to fairly wide, in the larger valves broadening

somewhat into a central area (Fig. 7 M–P); in the smaller valves (Fig. 7 R–T) there is scarcely any demarcation between axial and central area (cf. Bristol, 1920, text-fig. 8, fig. 16). Branches of the raphe in a more hyaline portion of the axial area (apparently a local thickening of the membrane). Two slit-shaped processes passing from the central nodule to the same side of the valve. Striae all radial, the central ones more prominent, less dense (approx. 20–25 in 10 μ) and more clearly punctate than the more apical striae (approx. 25–30 in 10 μ). A longitudinal line crossing all the striae and running close to the margin of the axial and central areas, commonly bent outwards opposite the central nodule. In the smallest valves the striae are parallel over a great part of the valve (Fig. 7 T) and such cells might belong to the species or to var. *relicta*, since the smallest valves of the latter are barely gibbous (Fig. 7 U).

var. *relicta* (McCall) (*N. terricola* Bristol pro parte). Fig. 7 U–W. Valves (15–30 μ l.; 4–5 μ br.) centrally gibbous. Areas and longitudinal line as in the species. Striae (centrally about 20–25 in 10 μ; apically approx. 25–30 in 10 μ) as in the species centrally but becoming parallel to weakly convergent near the apices.

var. *relicta* f. *triundulata* n.f. Margins triundulate and apices broadly rounded (Fig. 7 X). Very rare. Krasske (1938, p. 514) has recorded a var. *undulata* of *N. gibbula* Cleve from Iceland (valves 25–27 μ l.; 5–6 μ br.), but makes no mention of any differences in the orientation of the striae which are, therefore, presumably all radial.

While the *N. gibbula* Cleve of Hustedt (1924) and all earlier workers has an arctic or northern European distribution, that of Petersen (1935) has a wide distribution on European soils (Hustedt, 1935, pp. 385, 400; Bristol, 1920; Fehér, 1936*a*, *b*) and can hardly be classed as a glacial relict (Hustedt, 1924; McCall, 1933, p. 219). Though neither the species nor the variety ever occurred in abundance, they are both true soil diatoms, being present on sixteen soils.

(28) *Navicula muralis* Grun. f. *agrestis*, (Hust.) (incl. *N. agrestis* Hustedt, 1937–8). Fig. 8 A–I

The valves (5–8 μ l.; 2–3 μ br.) are elliptical, rarely somewhat rhomboid (Fig. 8 I). The length-breadth ratio in the larger valves is about 3 : 1, in the smaller 2 : 1. The very narrow axial area widens very slightly into a barely discernible central area (cf. Hustedt, 1937–8, pl. 20, fig. 21). The striae are radial, apart from one or two opposite the central nodule.

N. pseudomuralis Hustedt (1937–8, p. 245, pl. 19, figs. 25–27), *N. muralis* Grun., *N. agrestis* Hustedt (1937–8, p. 246, pl. 20, figs. 21, 22) and *N. atomus* (Naeg.) Grun. sensu Hustedt (see p. 74) are four minute elliptic species differing in the degree of radiation of the striae. This difference is sometimes small and can be expressed by comparing the more acute of the two angles made by the imaginary bisection of the apical axis by the more radial of the striae. Thus, in the order given above, the acuter of the angles are approximately 90, 85, 75 and 55°. *N. pseudomuralis* (20–25 str. in 10 μ) is further distinguished from *N. muralis* (30 str. in 10 μ) by the coarser, less dense striae. *N. agrestis*, an aerial species from Sumatra, stands closer to *N. muralis* than to the strongly radially striated *N. atomus* sensu Hustedt, who (1937–8) states that it differs from *N. muralis* in having valves which are narrower for an equal length. The larger valves of *N. muralis* f. *agrestis* agree well with Hustedt's *N. agrestis* in this as in other features but, with decreasing size, the valve becomes, as is the general rule, relatively

broader, so that, in the smaller cells, the length : breadth ratio is the same as in *N. muralis* (2 : 1; cf. Hustedt, 1930, p. 288; Cleve, 1894–5, pt. 2, p. 4). Doubtless this would have been found to be the case in *N. agrestis* (valves 8–11 μ l.) if Hustedt had seen the smallest valves. This soil diatom, therefore, connects *N. muralis* with *N. agrestis*,

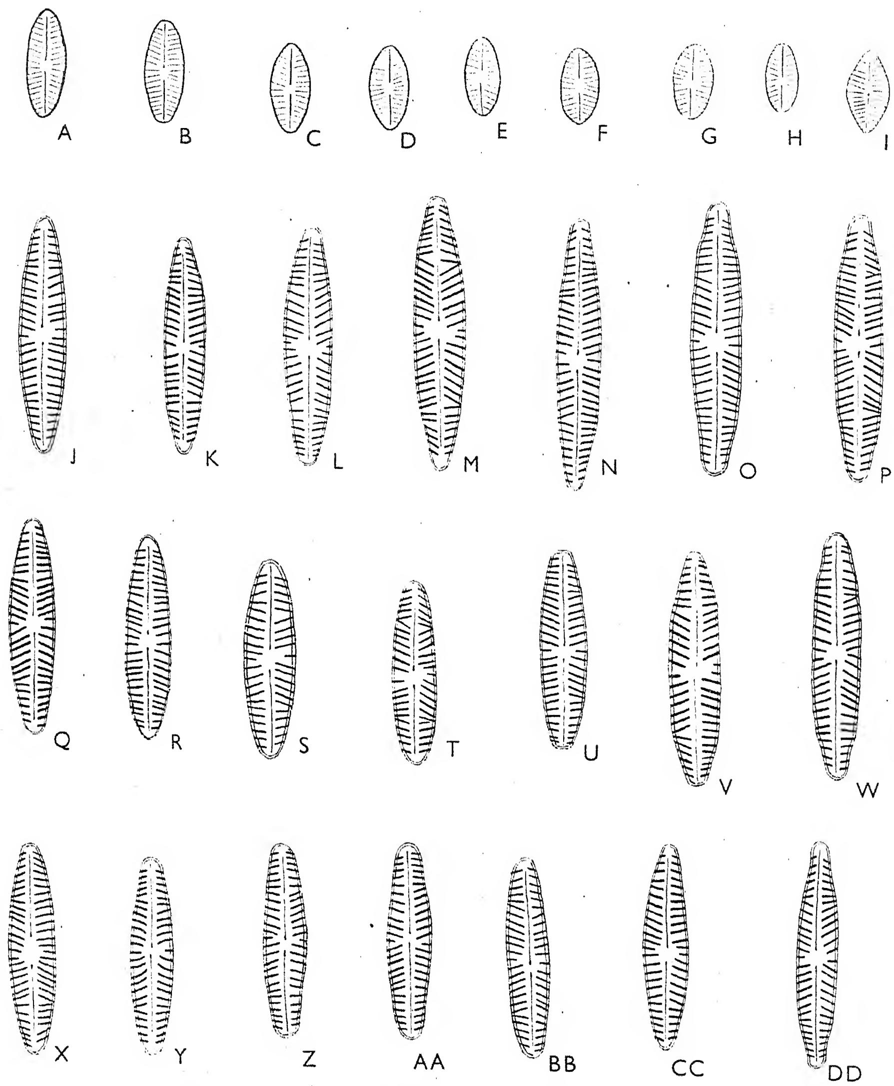

Fig. 8. A–I, *Navicula muralis* Grun. f. *agrestis* (Hust.); J–DD, *N. tenelloides* (Hust.) emend. All × 1750.

and the latter can hardly be considered as more than a form of the former, differing in the larger valves being slimmer than those of *N. muralis* and in the more strongly radial striation of all the valves. Petersen (1935) considers *N. muralis* to be mainly hydrophytic (he includes his record (1915) of *N. pelliculosa* (Bréb.) Hilse in this species) and Hustedt records it from bryophytes (1942). Present on three soils.

Naviculae lineolatae Cleve

(29) *Navicula tenelloides* (Hust.) emend. (incl. *N. cryptocephala* Kütz. var. *angusta* Boye Pet.). Fig. 8 J–DD

Valves (14–21 μ l.; 3–4 μ br.) linear-lanceolate, usually four to five times as long as broad with narrowly (Fig. 8 J, K) or broadly rounded (Fig. 8 T), rostrate (Fig. 8 O, P, W, DD) or, rarely, truncate (Fig. 8 U, V) apices. Branches of the raphe straight. Axial area very narrow, widening to a small usually rounded, though sometimes rectangular, central area, the shape of which varies according to the number of short striae to each side of the central nodule. Striae (16–19 in 10 μ) radial centrally and convergent apically, the transition from one type to the other often being very abrupt so that the two striae concerned form a V (Fig. 8 M); one of these striae may even lie isolated between the margin and the axial area (Fig. 8 P, T).

The soil specimens agree with Hustedt's (1937–8, p. 269, pl. 19, fig. 13; 1942, figs. 31–34) in the narrow linear-lanceolate valves, very narrow axial area, small more or less rounded central area and density of striae. Hustedt's (1942) European specimens are, however, more strongly radial and convergent than those from Java, in which feature they agree with Krasske's (1938, p. 514, unnumbered figure) from Iceland, while Hustedt's from Java form a connecting series. The apices may be broadly rounded as in Hustedt's Java specimens or rather narrowly so as in Krasske's specimens. They differ from previously described specimens in the presence of valves with apices which are sometimes rostrate or truncate, though Hustedt's (1942) German specimens may be almost rostrate (e.g. 1942, figs. 33, 34). I have not separated the forms as they grade into one another, though, in any one soil, one form often predominates over the others.

Petersen's (1928, p. 399, fig. 21) *N. cryptocephala* Kütz. var. *angusta* clearly belongs to the truncate type of this species. Other species which may be confused with it are:

N. Suchlandti Hustedt (Schmidt's *Atlas*, *99–100*, pl. 399, figs. 24–28) has bluntly cuneate apices, parallel margins and similarly striated valves. However, though the striae (15–16 in 10 μ) are little wider apart than in *N. tenelloides* the valves are shorter and narrower (11–14 μ l.; 2·5–3 μ br.).

N. radiosa Kütz. var. *tenella* (Bréb.) Grun. (Hustedt, 1930, p. 299; 1937–8, p. 269) differs in the more lanceolate and longer valves (25–65 μ l.).

N. bryophila Boye Pet., another aerial species, shows a rather similar series of valve shapes (Hustedt, 1937–8, pl. 18, figs. 18–23), but all the striae (35 in 10 μ) are radial.

N. pseudotenelloides Krasske (1938) agrees so closely with this species, apart from the less dense striae (14 in 10 μ), that there seems little justification for making it a separate species. It occurred in mosses and a brook.

The linear-lanceolate valves of this species are similar to those of *N. cincta* (Ehr.) Kütz. but differ in the finer denser striae, which are clearly of a different type in that they appear relatively faint and matt, while those of *N. cincta* are prominent and shining. There is no robust isolated central stria in *N. tenelloides*. The soil specimens of *N. cryptocephala* Kütz. are more lanceolate, length for length, with the radial striae curved.

Though rarely occurring in large numbers, this is a common soil diatom (present on twenty-three soils).

(30) *Navicula cincta* (Ehr.) Kütz. var. *Heufleri* Grun. (incl. f. *curta* Boye Pet.; Petersen, 1915). Fig. 9 A–G

The soil specimens have the markedly coarser and slightly less dense striae shown by the aquatic ones of this variety. However, while the latter apparently retain the linear-lanceolate form of the valves with decreasing size, the valves (8–28 μ l.; 4–10 μ br.) of the soil form become more elliptic (Fig. 9 D, E) and even oval (Fig. 9 F). The soil specimens also differ in the striation which is either radial centrally and parallel to weakly convergent near the apices (Fig. 9 A–C) or, in the smaller valves (Fig. 9 F), entirely radial. Very rarely large valves have all the striae radial (Fig. 9 G; cf. Carter, 1933, fig. 15, no. 18). The valves may be broader than recorded for the species (5–6 μ br., Hustedt, 1930). In the larger valves, the central striae do stand farther apart from their neighbours as is characteristic for the species, though they are not always clearly coarser than the rest (e.g. Fig. 9 A). In the smaller valves one or both these features may be lost (Fig. 9 D–F).

There is every gradation between the variety and the form *curta* (Petersen, 1915, pp. 291, 356, figs. 14, 15) which only consists of the smallest-sized cells. The soil forms should perhaps be considered as a separate species (cf. Petersen, 1935, p. 146), differing chiefly in the change of form and striation with decreasing size.

On eleven soils, all of which were not deficient in bases and contained appreciable amounts of $CaCO_3$. Petersen (1928, 1935) considers it to be a pronounced terrestrial form.

(31) *Navicula cryptocephala* Kütz. f. *terrestris* n.f. Fig. 9 H–W

Valves (13–23 μ l.; 4–6 μ br.) elliptic-lanceolate to lanceolate, margins typically convex (Fig. 9 H–L), but occasionally almost parallel centrally (Fig. 9 P, Q); one margin may be flattened centrally while the other is weakly convex, so that the valve has a *cymbelloid* appearance (Fig. 9 N, O, R, S). Apices sharply (Fig. 9 L) or obtusely (Fig. 9 N, O, R–U) rounded, sometimes weakly rostrate (Fig. 9 P, Q, U–W). Axial area narrow, central area transapically dilated. Branches of the raphe straight. Striae (15–20 in 10 μ) curved and radial except near the apices, where they are straight and parallel to weakly convergent.

The form differs from the species in the usual absence of rostrate apices, apical striae sometimes parallel and the occasional almost *cymbelloid* valves. The latter feature only occurred on enriched samples. There were all gradations between the various types of valve.

The valves of *N. cryptocephala* and its vars. *veneta* (Kütz.) Grun. and *exilis* (Kütz.) Grun. (Hustedt, 1930, p. 295) are said to have more or less clearly rostrate apices and the apical striae convergent, while none of the striae are figured as curved. In the former variety the valves are described as scarcely drawn out, but the figure (Hustedt, 1930, fig. 497*a*) shows them as weakly rostrate (Rabenhorst (1864) describes them as 'sublate lanceolata, apicibus productis'). In Van Heurck (1880–5, pl. 14, see also van Heurck, 1899) var. *veneta* is described as having rostrate-capitate valves, but in the figure, drawn by Grunow, the valves are not even rostrate, the apical striae are parallel to barely convergent, while the rest are radial and somewhat curved. In pl. 8, fig. 3 of the same work, however, var. *veneta* is figured with slightly rostrate apices, but again the apical striae are parallel rather than convergent. *N.* (*veneta* var.?) *pumila* Grun. is figured by

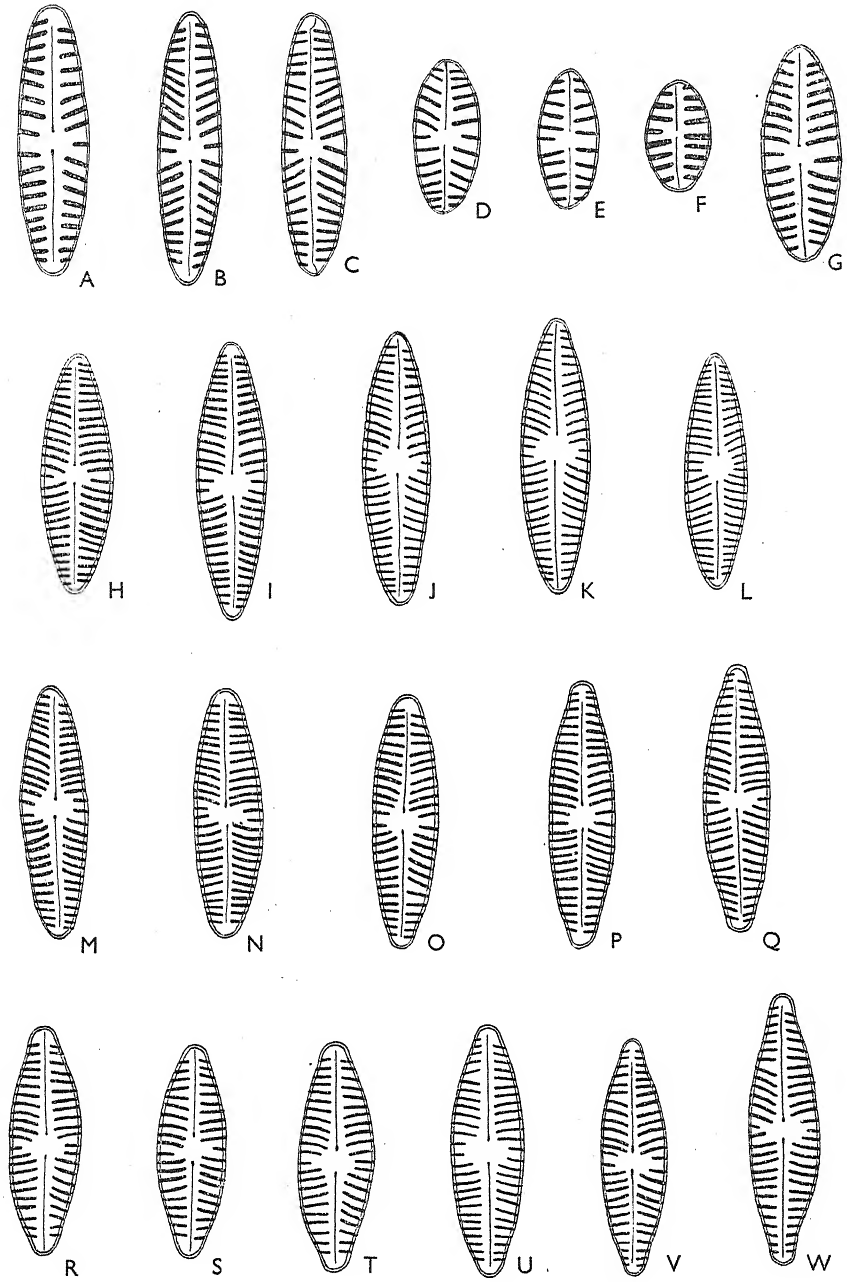

Fig. 9. A–G, *Navicula cincta* (Ehr.) Kütz. var. *Heufleri* Grun.; H–W, *N. cryptocephala* Kütz. f. *terrestris* n.f. All ×1750.

Grunow (Van Heurck, 1880–5, pl. 8, figs. 6, 7) as rhombic-lanceolate. Hustedt (1930) places var. *pumila* Grun. in var. *veneta*. There is, therefore, considerable confusion on these points, and the soil form might almost equally well be included in the species and the simplification in the form of the valves be connected with decreasing size.

Skvortzow (1937, pp. 327, 328) describes the valves of vars. *exilis* and *veneta* as 'slightly elongate', but his figures (pl. 7, fig. 5; pl. 9, fig. 9) show a valve with all the striae clearly radial, a feature neither described nor figured elsewhere, so that it is doubtful whether his specimens belong to this species.

The valves without rostrate apices are hardly to be distinguished from those of *N. menisculus* Schumann (Hustedt, 1930, p. 301, fig. 517; valves, 18–50 μ l.; 8–12 μ br.), apart from their constantly much smaller size and less markedly convex margins. Cleve (1894–5, pt. 2, p. 18) states that *N. menisculus* Schumann (*N. peregrina* (Ehr.) Kütz. var. *menisculus* Schum.) 'seems to pass into *N. cryptocephala* var. *veneta*'.

N. aliena Krasske (1938, figs. 7, 8) differs in the smaller size, less dense striae and usually less rectangular central area. *N. adversa* Krasske (1938, fig. 6) differs in the last-mentioned feature and the absence of even weakly capitate apices.

The valves without rostrate apices may be distinguished from *N. cincta* var. *Heufleri* (see p. 86), with which this species almost always occurs, in the less prominent and denser striae which are usually clearly less convergent near the apex, and by the greater width of the central area. Further, the striae in *N. cincta* var. *Heufleri* are usually not curved and are of a different type in that they appear more prominent and shining. Those of *N. cryptocephala* f. *terrestris* are like those of *N. tenelloides* (for the difference from which see p. 85) in their less prominent and matt appearance.

Present on eleven soils and appears, like *N. cincta* var. *Heufleri*, to be a calcicole. The species is previously recorded from soils (Petersen, 1915, 1928, 1935; Gistl, 1931–2; Fritsch & John, 1942). It is often abundant on drying mud at the edges of ponds (Lund, 1942, Table 1) and springs (Petersen, 1932).

Pinnularia Ehr.

The differentiation of the species of this genus is notoriously difficult (cf. Hustedt, 1930, p. 313), and this is especially so in the small soil specimens.

Capitatae

(32) *Pinnularia saxicola* n.sp. Fig. 10 G–I

Valves (11–16 μ l.; 3·5–4·5 μ br.) with weakly convex or parallel margins, clearly capitate in the largest cells (Fig. 10 G) and becoming progressively less so with decreasing size, the smallest being only weakly capitate or rostrate (Fig. 10 H, I). Branches of the raphe bending towards the same side of the valve in the region of the central nodule. Axial area narrow, passing very sharply into the central fascia in the smaller valves (Fig. 10 I) and more gradually in the larger (Fig. 10 G). Central fascia large, occupying a third or slightly less of the length of the valve. Striae (18–20 in 10 μ) with truncated ends and convergent apically. In the larger valves (Fig. 10 G) two or three of the striae bounding the central fascia on each side are radial, and the one nearest the central nodule may be shorter and narrower than the rest. In the smaller valves all the striae are convergent or one or two bounding the central fascia are parallel (Fig. 10 H, I).

The larger valves show some similarity in shape to *P. globiceps* Greg. var. *Krookei* Grun. (Hustedt, 1930, p. 319) but differ in striation, the central fascia and curved branches of the raphe. The flattening of the end of the stria abutting on the axial area

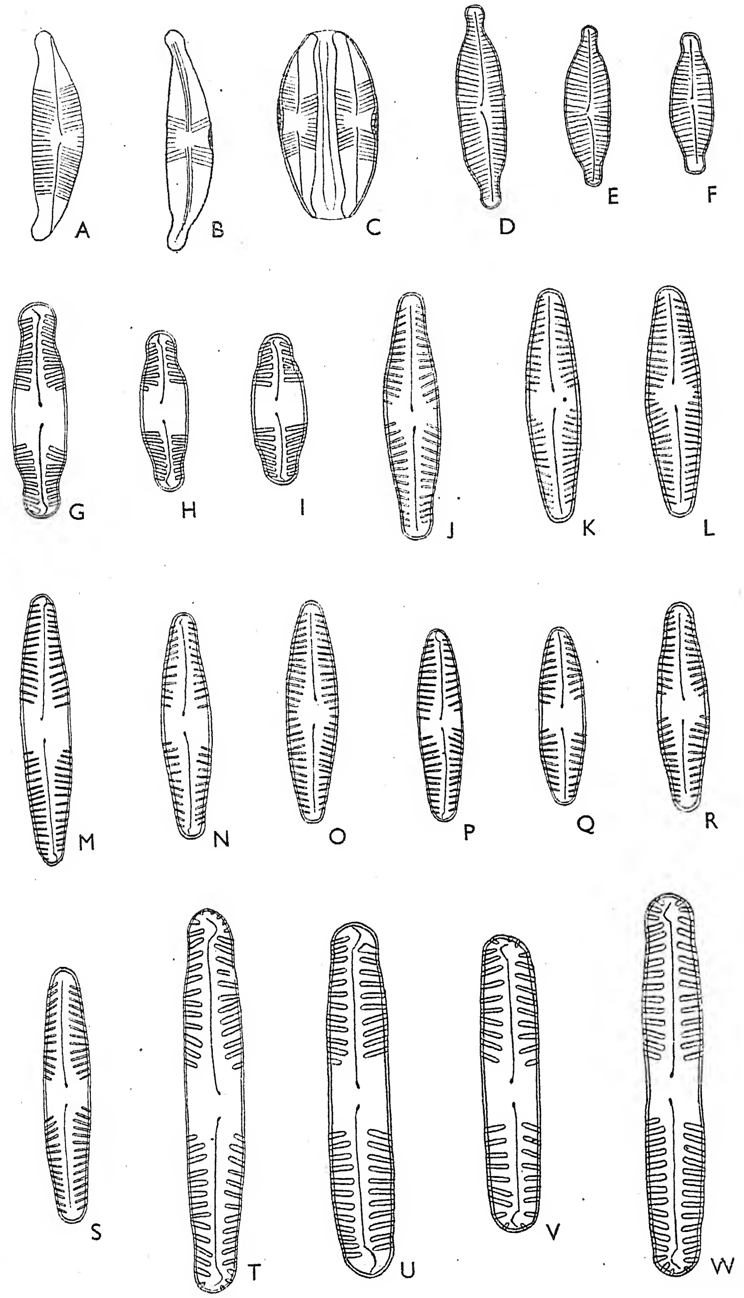

Fig. 10. A–C, *Amphora montana* Krasske; D–F, *Cymbella microcephala* Grun. f. *sublinearis* n.f.; G–I, *Pinnularia saxicola* n.sp.; J–S, *P. silvatica* Boye Pet.; K, L, two valves of one cell. T–V, *P. subcapitata* Greg.; W, ibid. var. *constricta* Hust. More apical striae not shown in A–C. All ×1750.

together with its greater width in some striae is a feature also seen in some striae in *P. intermedia* (p. 92).

From the base of an old brick wall together with *Navicula mutica* and *Achnanthes* sp. Probably aerial rather than terrestrial.

(33) *Pinnularia silvatica* Boye Pet. (Petersen, 1935; *Navicula falaisensis* Boye Pet.; Petersen, 1915). Fig. 10 J–S

The British specimens show a good agreement with Petersen's though some are smaller and have denser striae.

The linear-lanceolate valves (13–23 μ l.; 4 μ br.) sometimes have weakly rostrate apices (Fig. 10 J, N, R). The axial area, never very narrow, widens either to a transapical fascia or a wide central area which may be broader on one side of the valve than on the other (Fig. 10 O; cf. Petersen, 1935, fig. 7). Both a fascia and a central area may be present in one frustule (Fig. 10 K, L). The valves often lie somewhat on their side so that they appear weakly *cymbelloid*. The striae (18–22 in 10 μ) are strongly radial centrally and convergent apically.

This species shows some resemblance to *P. appendiculata* (Agardh.) Cleve (cf. Petersen, 1935, p. 147), of which it may only be a variety, differing in the relatively shorter, more lanceolate valves, the transition in breadth from the centre to the apices being usually more abrupt than in *P. appendiculata*. It may be distinguished from all but the smallest specimens of *P. microstauron* by the much finer striae, which may or may not be present opposite the central nodule (all the soil specimens of *P. microstauron* possessed a transapical fascia). From the smallest valves of *P. microstauron* they differ in the greater diminution in width from the centre to the apex (cf. fig. 120, P).

Present on three acid woodland soils (S 15, 17, 46) and from an enriched sample of a fourth (SE). Only found once previously by Petersen (1935) in a spruce wood. It seems, therefore, that it is an eu-terrestrial species typical of acid woodland soils.

(34) *Pinnularia subcapitata* Greg. Fig. 10 T–V

21–39 μ l.; 4–5 μ br.; 11–13 str. in 10 μ. Some of the smaller valves are wholly linear (Fig. 10 V), but the difference would seem to be connected with decreasing size, and there was every transition between those with and without capitate apices.

Common on base-deficient but not strongly acid soils (fifteen samples), often with *P. microstauron*; never abundant.

var. *constricta* Hustedt (1937–8, p. 288; no figure). Fig. 10 W

Differs in being transapically constricted. Occurred in company with typical specimens of the species and only in enriched samples.

Petersen's var. *sublanceolata* (1928, p. 409, fig. 30*a*) would appear to belong equally well to *P. microstauron*.

Divergentes

(35) *Pinnularia molaris* Grun. Fig. 11 J?, K ?, H, I, L–O.

Petersen (1928, p. 407) mentions the great resemblance between this species and small forms (e.g. f. *diminuta* Grun.) of *P. microstauron* (Ehr.) Cleve var. *Brébissonii* (Kütz.) Hust. (*P. Brébissonii* Kütz.). From Hustedt's description and figure (1930, p. 316, fig. 568), the only distinction seems to be the denser striae in *P. molaris* (15–20 in 10 μ;

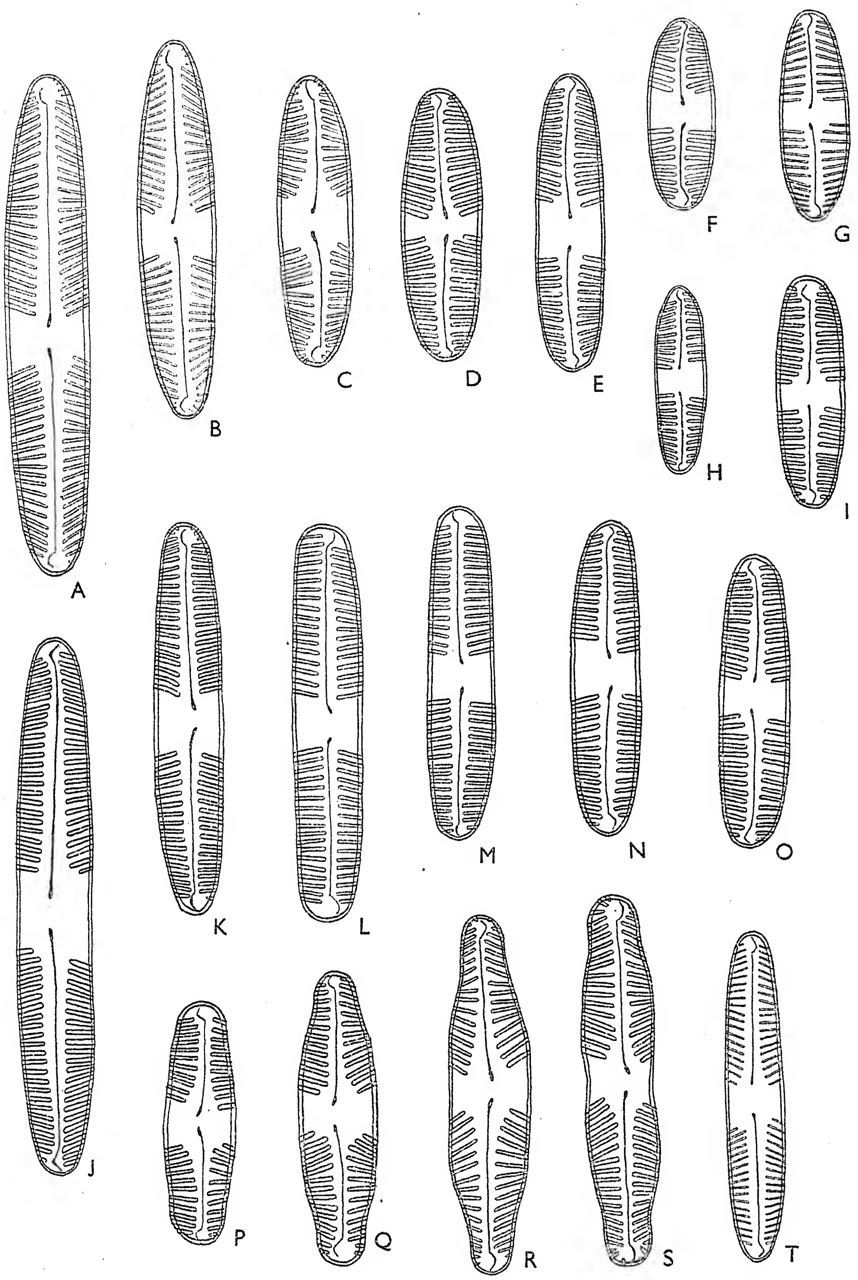

Fig. 11. A–E, *Pinnularia microstauron* (Ehr.) Cleve (near var. *Brébissonii* (Kütz.) Hust. and f. *diminuta* Grun.); F, G, J, K, specimens intermediate between *P. microstauron* and *P. molaris*; H, I, L–O, *P. molaris* Grun.; P–T, *P. microstauron* (Ehr.) Cleve; S, ibid. f. *biundulata* O. Müll. All $\times 1750$.

P. microstauron, 10–13 in 10μ), but the soil specimens of *P. microstauron* may have denser striae (13–20 in 10μ) than recorded for aquatic habitats. Petersen (1928) distinguishes *P. molaris* by the almost parallel striae. My specimens (valves 23–42μ l.; 5–6μ br; 14–20 str. in 10μ) differ typically from those of *P. microstauron* in the less

markedly radial central and convergent apical striae, the central ones being, at the most, only slightly shorter than the rest, so that the transition from axial to central area is more abrupt than in *P. microstauron*. The valves are also generally more linear. There are, however, transitional forms between the two species, some of which cannot be relegated to either with certainty (e.g. compare Fig. 11 A, B with 11 J, K; 11 C–E with 11 M–O). Petersen's specimen (1928, fig. 26*b*) forms a transition to *P. microstauron* in its elliptical valve and shortened central striae. It is in the smaller valves that differentiation is particularly difficult, the linear-lanceolate form of the larger valves of *P. molaris* being lost (e.g. Fig. 11 H, I). Transitional cells occur (Fig. 11 F, G) in which the transition from axial to central area differs on each side of the valve (Fig. 11 F), while a more or less '*microstauron*' transition may be combined with parallel central and strongly convergent apical striae (Fig. 11 G).

Even if these are two separate species their retention in two sections of the genus (Cleve, 1894–5; Hustedt, 1930) cannot be upheld even in the aquatic specimens where the striation of *P. molaris* is by no means parallel.

P. molaris, as defined above, appears to favour soils which are not base-deficient. It was never common (eleven samples).

(36) *Pinnularia microstauron* (Ehr.) Cleve. Figs. 11 A–E, P–T; F, G, J?; 12 O, P; 18 B–E

I follow Hustedt (1930) in including *P. Brébissonii* Kütz. in this species. Its relationship to *P. molaris* and distinction from *P. intermedia*, and *P. silvatica* are discussed under those species.

The soil forms (valves 14–39 μ l.; 5–7 μ br.) show all gradations between the species and vars. *Brébissonii* (Kütz.) Hust. (incl. f. *diminuta* Grun. and *linearis* O. Müll.) and *biundulata* F. Müll. All the soil specimens possessed a transapical fascia. The striae (13–20 in 10 μ) vary in width (compare Fig. 11 A–D; Fig. 18 B–E) but, except in the smallest valves, are strongly radial centrally and strongly convergent apically. One or more of the four striae bounding the central area are often wider than the rest (Fig. 11 B; cf. McCall, 1933, p. 258).

This is one of the commonest (present on thirty-two soils) and, sometimes, one of the most abundant soil diatoms on well-cultivated soils which are neither alkaline nor very strongly acid (*p*H 4·7–6·6). It is recorded by Cleve (1894–5, pt. 2, *P. Brébissonii* Kütz.) from earth and mosses.

(37) *P. intermedia* Lagerst. (incl. *P. obscura* Krasske, 1932). Fig. 12 A–J

Valves 12–35 μ l.; 4–5 μ br.; 9–12 str. in 10 μ. This species would appear to belong to this section of the genus.

Petersen (1928, p. 405) has given five characteristics common to all forms of the species. My specimens differ in that, first, one or more of the four striae bounding the central fascia are occasionally shorter than the rest (Fig. 12 C, D). This is Petersen's characteristic no. 2 (see also his reference to Lagerstedt's pl. 1, fig. 3 *a*, 1873, and Bristol's text-fig. 8, figs. 6, 8, 1920). Secondly, that, not only may the striae be almost parallel in the smaller forms but they may even be convergent, with the exception of the shortened central stria or striae (Fig. 12 J). Thirdly, long lanceolate valves occur (early descendants

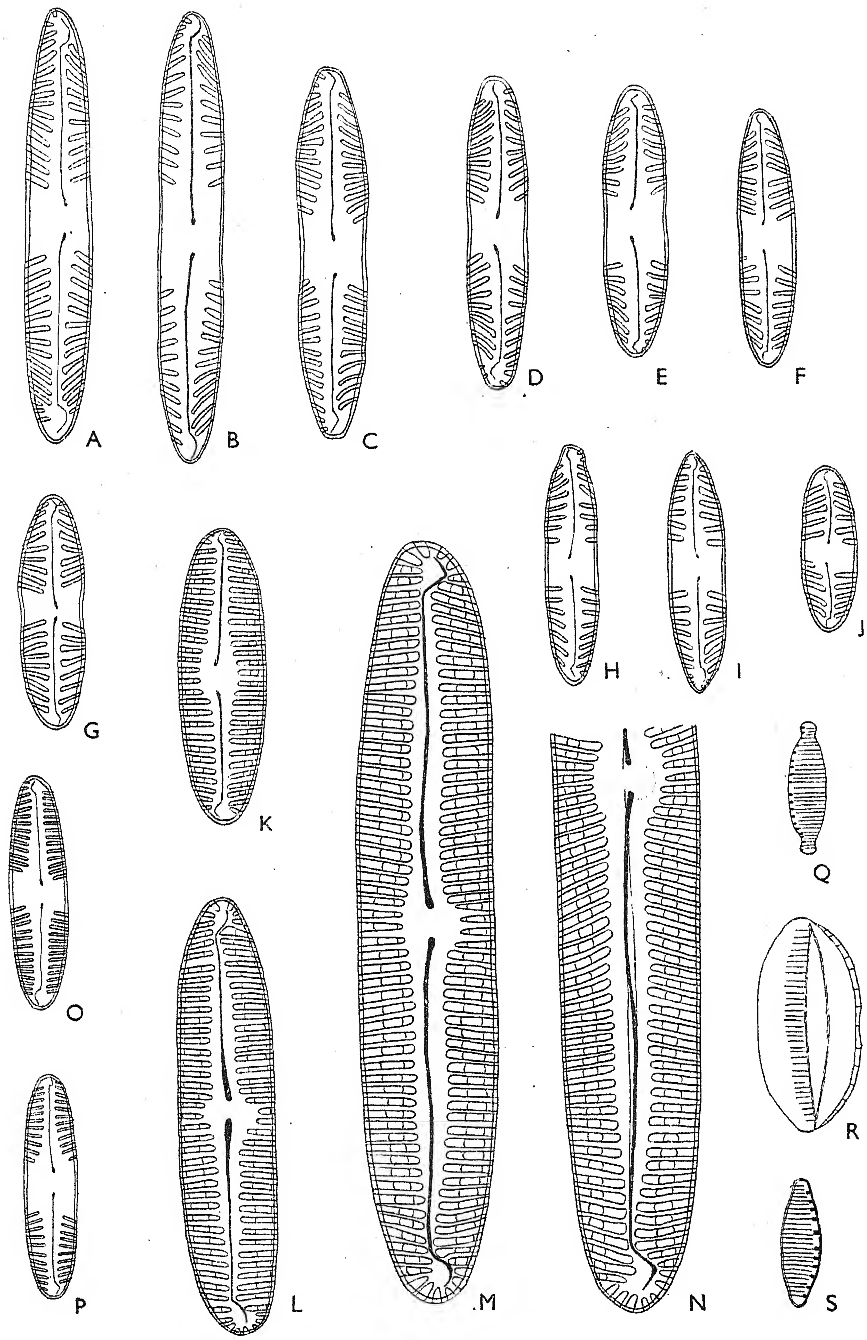

Fig. 12. A–J, *Pinnularia intermedia* Lagerst.; K–N, *P. viridis* (Nitzsch.) Ehr.; O, P, *P. microstauron* (Ehr.) Cleve; Q, *Nitzschia microcephala* Grun.; R, *N. Tryblionella* Hantzsch. var. *debilis* (Arnott) A. Mayer; S, *N. fonticola* Grun. All × 1750.

of auxospores?), while I have not observed forms with strongly truncate or truncate-capitate apices (Petersen, 1928, fig. 24 *d*, *e*).

Petersen's (1928) fig. 6 is considered as a form of a separate species by Krasske (1932, p. 117)—*P. obscura*—differing only in the central constriction and markedly cuneate apices to the valves (cf. Petersen, 1935). *P. obscura* itself, however, contains specimens (e.g. Krasske, 1932, fig. 22*a*) only differing from *P. intermedia* in the more numerous striae (15 in 10 μ) and smaller size, while constricted weakly cuneate valves are recorded by Lagerstedt (1873, pl. 1, fig. 3*a*). As there appear to be all transitions between the constricted cuneate specimens and the other types (see Fig. 12 A–F), it seems to me that *P. obscura* should be included in this species.

In addition to some of the striae commonly being wider near the raphe than near the margin of the valve (Petersen's characteristic no. 4; my Fig. 12 A, C, D, G, I), the apical ones are often not only markedly convergent but also curved (Fig. 12 A–E).

The elongate lanceolate valves (Fig. 12 A, B) differ from similarly shaped valves of *P. microstauron* in the feature mentioned in the preceding paragraph and in the less dense striae (9–12 as against 13–20 in 10 μ), which are either not or are less markedly shortened around the central fascia; the valve, too, has more pointed or more or less cuneate apices and is thinner relative to its length.

Lagerstedt's (1873, pl. 1, fig. 3*a*) linear specimen resembles *P. microstauron* apart from the difference in the density of the striae.

One of the commonest soil diatoms (on thirty-four soils), commonly occurring with *P. microstauron* in somewhat acid soils, though less abundant.

Distantes

(38) *Pinnularia borealis* Ehr. Fig. 13 E

Valves 22–46 μ l.; 5–8 μ br.; 5–6 str. in 10 μ. For variation in form see Petersen (1928, p. 402).

Though present on thirty-two soils from *p*H 4·4 to 8·0, it never occurred in large numbers. It was one of the few species occurring on both base-deficient and calcareous soils poor in phosphates, nitrates and potash. It never grew well in cultures or enriched samples. It seems to be a highly xerophytic species for Petersen (1928) states that it stands desiccation well and Bristol (1920) found it in nine cultures made from air-dried soils, while Krasske (1932) and Beger (1927, 1928) record it as typical of xerophytic mosses and on thatched roofs. I have also found it to be a common inhabitant of moss tufts. This may account for its regular occurrence on the more sandy soils.

(39) *Pinnularia viridis* (Nitzsch.) Ehr. Fig. 12 K–N

This is one of the largest soil diatoms (valves 22–94 μ l.; 6–13 μ br.; 8–12 str. in 10 μ), even though most of the specimens are nearest to var. *diminuta* Mayer. The striae, in the smallest valves, are almost parallel (Fig. 12 K, L), the degree of radialness and convergence increasing with increasing size (Fig. 12 M, N). The compound nature of the raphe can only be seen in the largest valves (Fig. 12 N).

Occurred in small numbers on fourteen soils, chiefly those which were well cultivated and somewhat acid. Fritsch & John (1942) record it from four soils, and Petersen (1928) found var. *commutata* Grun. not uncommon in Iceland on earth. It is often common on drying mud at the edges of ponds (Lund, 1942, table 1).

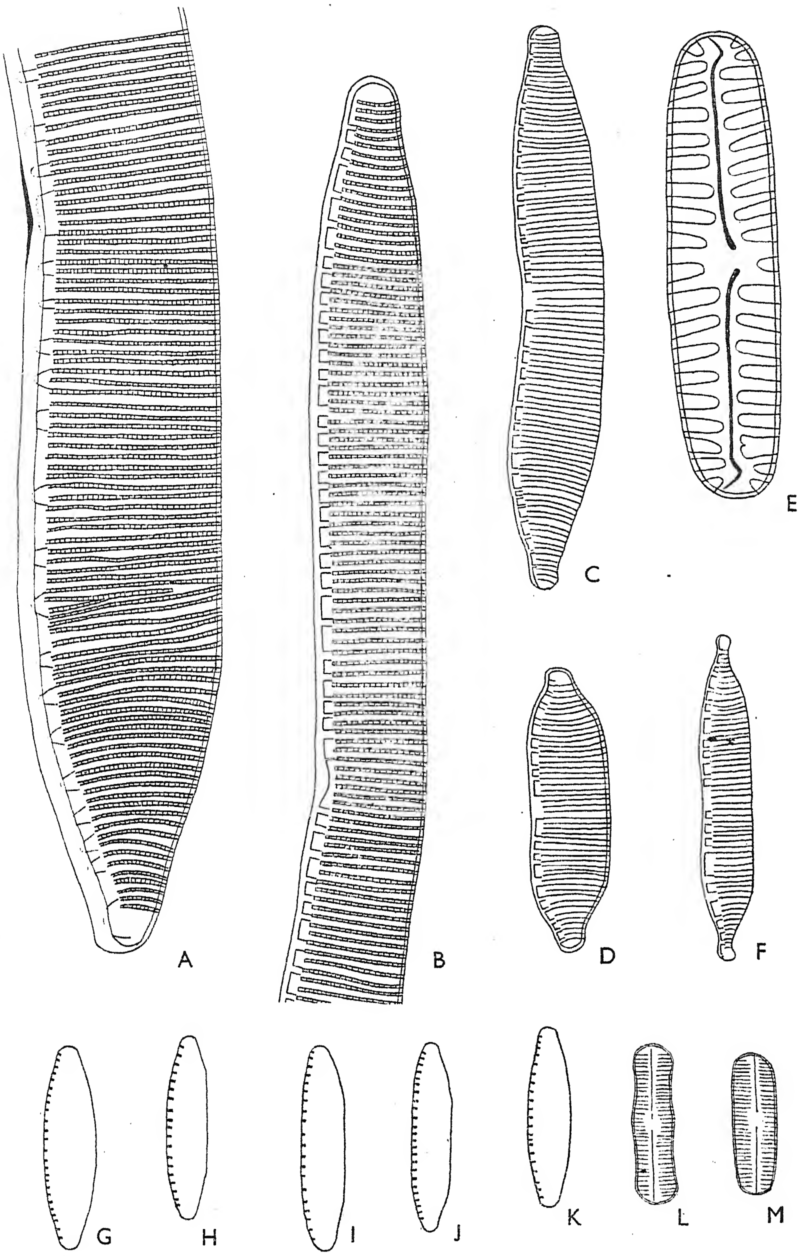

Fig. 13. A–D, F, *Hantzschia amphioxus* (Ehr.) Grun.; E, *P. borealis* Ehr.; G–K, *Nitzschia communis* var. *hyalina* n.var.; L, *Navicula contenta* Grun.; M, ibid. f. *parallela* Boye Pet. All ×1750.

var. *sudetica* (Hilse) Hust. Fig. 18 A

This variety, well known from mountainous districts, occurred on two very acid mountain soils (S22, 27). Valves 46–51 μ l.; 9–10 μ br. The striae (12–16 in 10 μ) are narrower and denser than in the species and have less clear longitudinal lines.

Amphora Cleve

(40) *Amphora montana* Krasske. Fig. 10 A–C

The soil specimens (valves 14–18 μ l.; 3·5–4 μ br.) agree with those of Krasske (1932, p. 119, fig. 27), apart from the fact that the central area does not always reach the dorsal margin and the striae on each side are radial as shown by Hustedt (1937–8, pl. 24, figs. 6–8), with the exception of the short central striae on the dorsal side. These latter are parallel, farther apart from one another, and more prominent than the rest. All the striae are very fine and so difficult to resolve near the apices, those on the dorsal side being denser (approx. 35 in 10 μ) than those on the ventral side (approx. 30 in 10 μ). The central dorsal striae appear to lie in a concavity so that a dark area occurs at this point (Fig. 10 B), as is shown by Krasske (1932) and Hustedt (1937–8).

Occurred on twelve soils, occasionally in considerable numbers on the more calcareous soils. Hustedt (1937–8, p. 413) records it as occurring in alkaline waters (*p*H 7·3–8·6) with a maximum development at *p*H 7·7.

Cymbella Agardh.

(41) *Cymbella microcephala* Grun. f. *sublinearis* n.f. Fig. 10 D–F

The soil specimens differ from the aquatic forms in either both margins of the valve (10–15 μ l.; 3–4 μ br.; 25–30 str. in 10 μ) being flat or only the ventral margin, the dorsal being then clearly convex, together with the clearly, though not strongly, radial striae. Var. *robusta* Hustedt (1938, p. 561) is even more markedly linear but differs in this and the larger size and smaller central area. The striae are also clearly radial. Hustedt states that the species is very variable.

Though never observed alive, the frustules occurred in slides and cultures from three soils. Hustedt (1938) records it as frequent on wet rocks.

Hantzschia Grun.

(42) *Hantzschia amphioxus* (Ehr.) Grun. Fig. 13 A–D, F

The figures show the wide range in size (17–110 μ l.; 4–15 μ br.), form and striation (14–25 in 10 μ; carinal dots 3–9 in 10 μ). The various forms are generally distributed.

The most ubiquitous of soil diatoms and recorded from soils all over the world. It was present on fifty-one soils, and though it did not commonly occur in large numbers its relatively large size must be taken into account from the point of view of biological productivity. Most common and abundant on alkaline soils but present from *p*H 5 to 8·2. Hustedt (1937–8) states that, though ubiquitous in waters from *p*H 5·5 to 9·24, the main development occurs in alkaline waters and strongly acid waters are shunned. For size relationships see Part I, E.

Nitzschia Hassall

The smaller species (sect. *lanceolatae*) are extremely difficult to separate from one another (cf. Hustedt, 1930, p. 412; 1937–8, p. 472), especially in cultures and enriched samples. Further, as is common in soil diatoms, the striae are very faint, and the density of these and the carinal dots cannot be trusted when comparing the soil with the aquatic forms, though they are valuable features in comparing the soil forms among themselves. The density of the striae and carinal dots form the main distinctive feature in many aquatic species (cf. Hustedt, 1930, 1937–8), though these themselves may show

considerable variation even in one cell. There is little doubt that more than one species has been described from soils under more than one name.

Tryblionellae

(43) *Nitzschia Tryblionella* Hantzsch. var. *debilis* (Arnott) A. Mayer. Fig. 12 R

The ribs generally could only be observed over part of the valve (14–21 μ l.; 6–8 μ br.; 18–20 ribs; 8–10 carinal dots in 10 μ).

This is a calcicolous species occurring on thirteen soils though never in large numbers. Recorded from English (Fritsch & John, 1942) and European (Petersen, 1935) soils.

Obtusae

(44) *Nitzschia parvula* Lewis var. *terricola* n.f. Fig. 14 A–I

This variety differs from the species (Hustedt, 1930, p. 421) in relatively and absolutely greater length of valve (25–70 μ l.; 4–5 μ br.), while the apices are less markedly diminished in breadth.

While the larger valves are clearly sigmoid and constricted centrally (Fig. 14 A–D), the smallest are either almost straight (Fig. 14 F, H) or more indented on one side (Fig. 14 G) than the other and are all barely sigmoid. Though the smallest valves are less than one-half the length of the largest, there is no appreciable difference in width between them (cf. *N. Hantzschiana*, p. 100). There is no visible central pore and the keel is strongly excentric, so that this species might be better placed in the *sigmoideae*. There are 6–9 carinal dots and 31–37 fine striae in 10 μ.

It differs from *N. obtusa* W. Smith var. *scalpelliformis* Grun. (Hustedt, 1930, p. 422) in the median constriction, more or less rostrate apices and absence of an incurved central portion of the keel. One of Van Huerck's figures (1899, pl. 16, fig. 538 left) and Bristol's (1920, p. 71, text-fig. 10, fig. 7) of var. *scalpelliformis* agree with *N. parvula* in a weak central constriction of the valve and Hustedt (Schmidt's *Atlas*, pl. 338, figs. 12–19) does not consider that such specimens can belong to *N. obtusa*. Petersen (1928, p. 418) and Beger (1927, p. 391) have also described small somewhat sigmoid *Nitzschiae* from soil and mosses.

Present in moderate numbers on one soil (S28).

(45) *Nitzschia ignorata* Krasske. Figs. 14 J, K; 15 A–G

This diatom agrees well with the species (Hustedt, 1930, p. 422, fig. 819) apart from the carinal dots appearing rectangular and not rounded.

Valves (31–44 μ l.; 3–4 μ br.) linear or linear-lanceolate, weakly (Fig. 15 B, C, F), sigmoid or almost straight (Fig. 15 A, D, E). Apices bluntly to sharply rounded (Fig. 15 B, F) and more or less rostrate. Cells in girdle view clearly sigmoid (Fig. 14 J, K). Keel sometimes not clearly strongly excentric (Fig. 15 A, B), usually with a clear central pore and incurved centrally in those valves having a slight central concavity of the keel-bearing margin (Fig. 15 A, B). Carinal dots (9–12 in 10 μ) somewhat larger and less dense centrally than near the apices. Striae faint (34–38 in 10 μ).

This variety differs from *N. obtusa* and its var. *scalpelliformis* in the lanceolate valves (cf. Hustedt, 1937–8, p. 487) and clearly sigmoid girdle view. The keel is more markedly excentric, the valves shorter and thinner with correspondingly denser carinal dots and

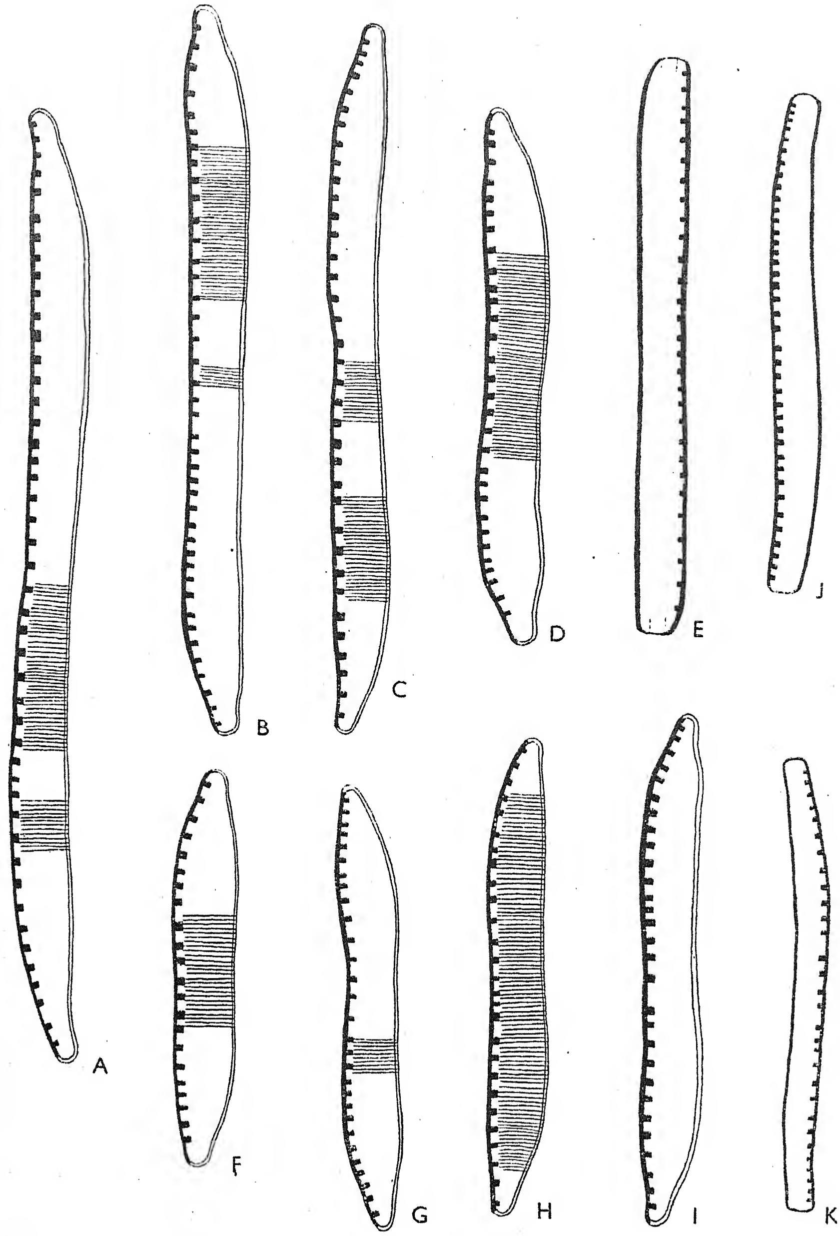

Fig. 14. A–I, *Nitzschia parvula* Lewis f. *terricola* n.f.; J, K, *N. ignorata* Krasske. E, J, K, girdle views. Striae shown in part only. All × 1750.

striae. It differs from *N. parvula* in the absence of a central constriction, slimmer, smaller valves, more sigmoid girdle view and often clearly less excentric keel.

Present on two soils (S 52, 8).

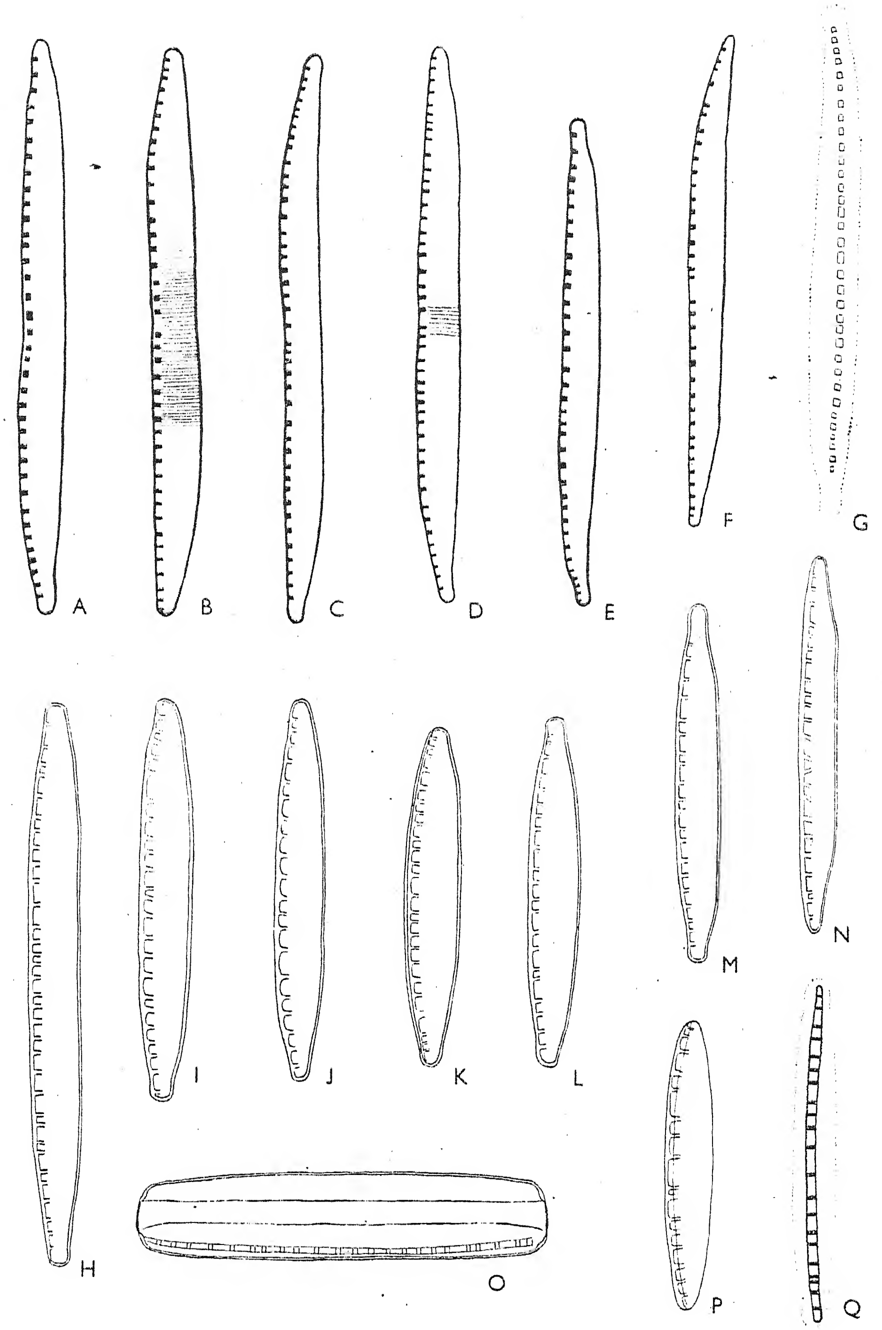

Fig. 15. A–G, *Nitzschia ignorata* Krasske; H–Q, *N. terricola* n.sp. G, Q, keel seen from above. O, girdle view. Striae shown in part only. All ×1750.

Dissipatae

(46) *Nitzschia terricola* n.sp. Fig. 15 H–Q

The linear to linear-lanceolate valves (21–43 μ l.; 3–4 μ br.) of the larger cells have more or less truncate to cuneate or rostrate apices, while, with decrease in length, the transition between central and apical portions becomes more gradual and linear-lanceolate valves may occur (Fig. 15 P). The keel is not so strongly excentric as in section *Lanceolatae* and is more like that in section *Dissipatae*. The carinal dots (7–12 in 10 μ) are large relative to the size of the valve and, occasionally, not parallel to one another (Fig. 15 N; cf. *N. recta* Hantzsch.). No striations were ever visible, which also points to the section *Dissipatae*. A pale longitudinal line passes across the carinal dots near their inner margin (indicated in Fig. 15 P).

Some of the valves resemble *N. recta* Hantzsch. (Hustedt, 1930, p. 411, fig. 785) in shape (e.g. Fig. 15 N) and in the carinal dots (see above), and this may possibly be a small variety of that species. Others show more resemblance to *N. dissipata* which is recorded by Petersen (1935, p. 150) from soil.

This was common (eleven samples) on soils containing appreciable quantities of $CaCO_3$, sometimes occurring in considerable numbers.

Lanceolatae

(47) *Nitzschia microcephala* Grun. Fig. 12 Q

Valves 10 μ l.; 3 μ br.; c.d. 14–15 and str. 28–30 in 10 μ.

A few cells were observed on slides, but this is probably not a soil diatom.

(48) *Nitzschia fonticola* Grun. Fig. 12 S

Valves 10 μ l.; 3 μ br.; c.d. 14 and str. 28–30 in 10 μ.

Observed once in a culture from a garden soil (S 1) and probably not a soil diatom.

(49) *Nitzschia Hantzschiana* Rabh. Fig. 16 A–U

Valves (10–40 μ l.; 2–4 μ br.) somewhat variable in shape. The largest (Fig. 16 E–H) rarely with one weakly concave margin, apices rounded and cuneate-rostrate (Fig. 16 E, F) to weakly subcapitate (Fig. 16 D, G). Valves of medium size commonly centrally constricted (Fig. 16 N–R, T) or concave on one margin. Apices becoming more cuneate with decreasing length of valve and always so in the smallest cells (Fig. 16 I–M) which are very rarely constricted or concave on one margin. Carinal dots prominent (9–14 in 10 μ including the central gap). The soil specimens differ from Hustedt's (1930, p. 414, fig. 797) description and figure in usually having a wider 'gap' between the two approximately central carinal dots than between those to each side of them (e.g. Fig. 16 B–D, H–J); sometimes the gap is no wider than over the rest of the valve (e.g. Fig. 16 N). This feature is, however, described by Cleve & Grunow (1880). The striae (27–30 in 10 μ) are relatively prominent and rarely curved near the apices (Fig. 16 O, Q).

The shorter valves are often not only relatively, but also absolutely wider than the longer (compare Fig. 16 D–H with I–M and N–Q with R, S, U).

There appear to be several races (compare Fig. 16 D–F; G, H; N–Q each from a different soil) differing in the breadth of the valves, density of the carinal dots, degree and frequency of the concave margin or central constriction and in the type of apex. They grade into one another, the smaller valves being especially similar.

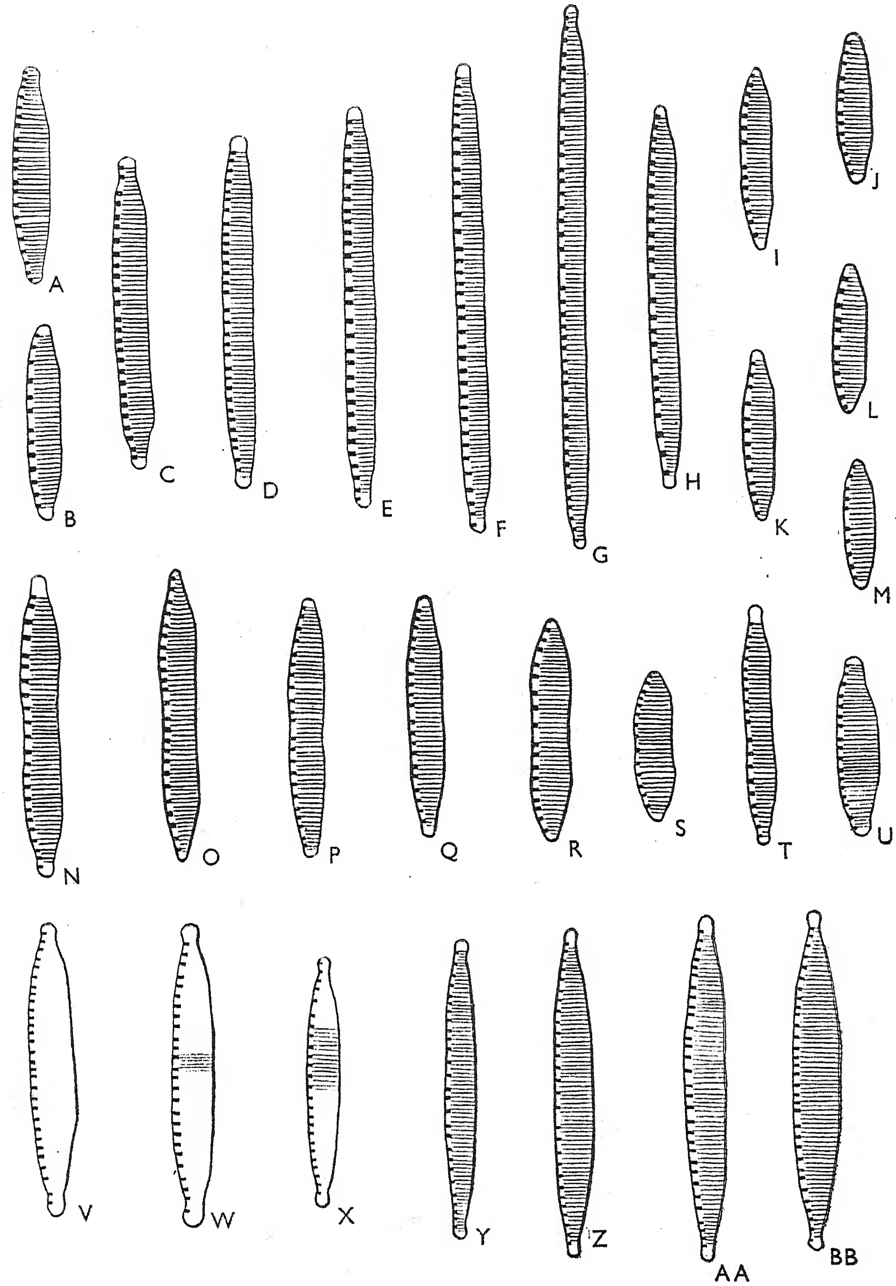

Fig. 16. A–U, *Nitzschia Hantzschiana* Rabh., V–BB, *N. palea* (Kütz.) W Smith. Striae shown in part in W, X. All ×1750.

The best taxonomic features are the relatively large carinal dots, the central 'gap', relatively prominent striae and the linear valves with more or less cuneately narrowed apices. It shows considerable resemblance to the rather variable *N. frustulum* (Kütz.) Grun. which seems to differ only in the more gradual decrease in size towards the apices but even this feature varies (Hustedt, 1930, p. 414), while var. *perminuta* Grun. (Hustedt, 1930, p. 415) is described as narrow-linear with 27–30 str. in 10 μ. In any case, differences in density of carinal dots and striae used for differentiating aquatic species are not applicable to forms occurring in soil. Hustedt's (Schmidt's *Atlas*, *88–89*, pl. 349, figs. 23–26) earlier figures of *N. frustulum*, showing valves with one concave margin or a central constriction, would appear to belong to this species.

Hustedt's (1937–8, p. 477, pl. 41, figs. 13–16) *N. Ruttneri* shows similarities to the largest valves of this species in being very narrowly linear (19–36 μ l.; 1·8–2·5 μ br.) with a barely detectable hint of a central 'gap'. The striae are, however, very fine (32–35 in 10 μ) even in those aquatic habitats, while the carinal dots are prominent (9–10 in 10 μ) and the valves have cuneate apices but no marginal concavity or constriction. Hustedt did not observe any valves comparable to the smaller ones here described.

Occurred in small numbers on six soils, but was very abundant in some of the enriched samples.

(50) *Nitzschia palea* (Kütz.) W. Smith. Figs. 16 V–BB; 17 A–R

The linear to linear-lanceolate valves (16–34 μ l.; 3–5 μ br.) may have the central portions of both margins flat or both may be weakly convex; very rarely one margin is centrally concave (Fig. 17 G). Usually the margin bearing the keel is more or less convex (Fig. 17 C–F), while the opposite margin is flat. The apices are usually truncate to rostrate (Fig. 17 D–H), but may be more or less clearly capitate (Fig. 17 A–C), especially in some of the more lanceolate valves (Fig. 16 V–BB). Sometimes the central part of the margin bearing the keel passes smoothly into the apical portion, while the flat opposing margin passes more abruptly and may show an indentation just behind the apex, so that the valve has an almost *cymbelloid* appearance (Fig. 17 D–F, L).

There are 12–15 carinal dots and 30–36 striae in 10 μ. The latter are very fine and occasionally invisible, though they are probably present. They may be curved near the valve apex (Fig. 17 C, I, K, M, N).

As in the preceding species, there appear to be two or three races of the species which grade into one another (compare Fig. 17 A–C with D, E and with Fig. 16 V, W, each from a different soil), but again they do so even in one and the same soil.

Though a few of the narrow linear forms (Fig. 16 X–AA) show some resemblance to the longer valves of the preceding species, they are never so long relative to their breadth nor so strongly linear, while the carinal dots and striae are not only denser but also less prominent, and there is no central 'gap' in *N. palea*. Decrease in length does not proceed so far as in *N. Hantzschiana*, and though the shorter valves may be relatively broader than the longer it does not appear that they are ever absolutely so. The shortest valves are relatively uncommon so that they may belong to a separate form, in part at least.

It will be seen that the variation in form is considerably greater than usually described for aquatic habitats (Hustedt, 1930, p. 416, fig. 801). Hustedt (Schmidt's *Atlas*, *88–89*,

pl. 349, figs. 1–10) shows valves with parallel margins and with one margin weakly concave.

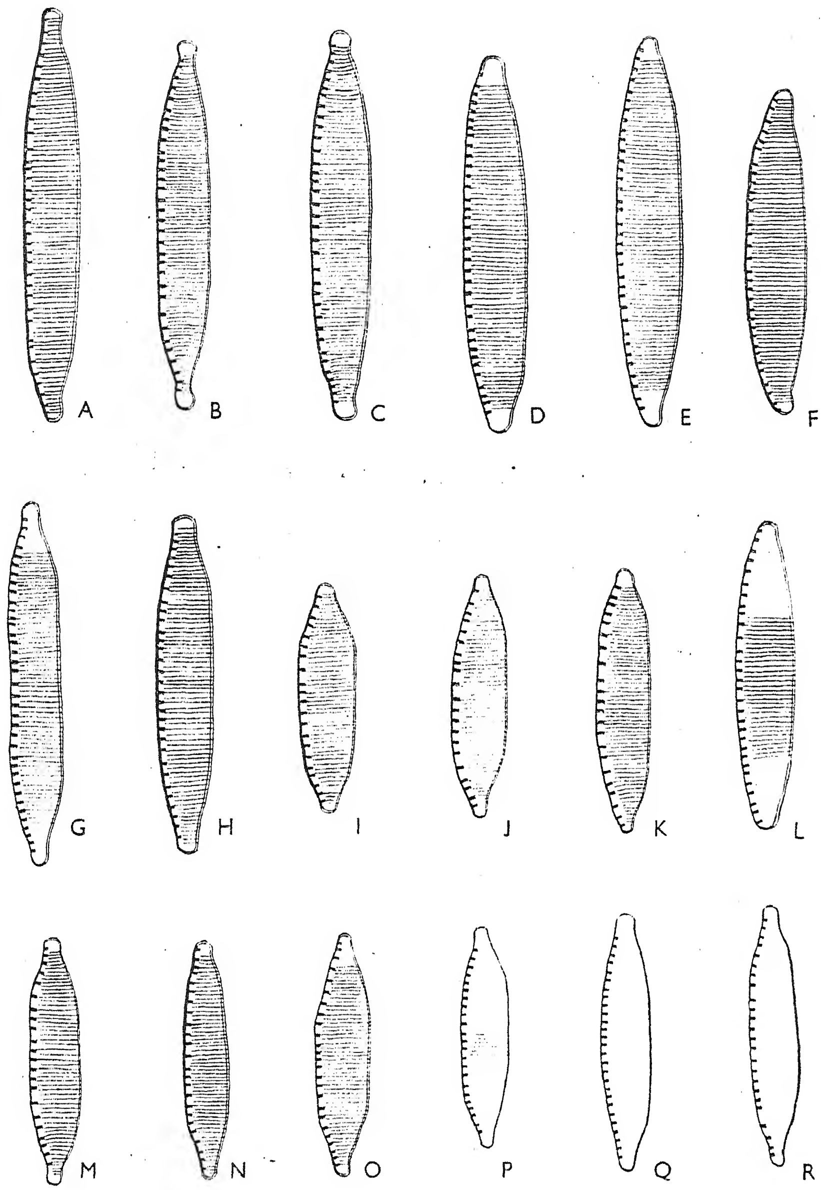

Fig. 17. *Nitzschia palea* (Kütz.) W. Smith. More apical striae not shown in D, E, L, P. All ×1750.

This is a common soil diatom (twenty-one samples), often occurring in large numbers, especially on well-cultivated soils. It is the only diatom recorded from old stored soils by Bristol (1919). It is often abundant on drying mud at the edges of ponds (Lund, 1942, table 1).

(51) *Nitzschia communis* Rabh. var. *hyalina* n.var. Fig. 13 G–K

The soil specimens (valves 13–15 μ l.; 2·5–4 μ br.) not only differed from the species in all being smaller than the smallest size recorded for the latter in aquatic habitats (20 μ l.; Hustedt, 1930, p. 417), but also in the constantly more numerous carinal dots (15–20 in 10 μ) and the absence of any visible striations. *N. communis* is recorded as having clearer striations than *N. palea*, in the soil specimens of which they were usually visible. Var. *abbreviata* Grun. (Cleve & Grunow, 1880, p. 97) is nearer in size to the soil specimens (6–13 μ l.; 2·6–3 μ br.; 12–14 carinal dots in 10 μ), though the carinal dots are less dense and the striae clearly visible (30 in 10 μ). This variety is said to be very like the more strongly striated *N. inconspicua* Grun. (Cleve & Grunow, 1880) into which Bristol (1920, p. 71) places specimens clearly belonging to the same species as mine. Petersen (1935, p. 151) says that Bristol's specimens may not be the same as his. It does not appear to me that these soil specimens can belong to *N. inconspicua*, which is said by Cleve & Grunow (1880, p. 99) to join *N. perpusilla* (Rabh.) Grun. and to be the smallest of the *N. Hantzschiana* group of species. Hustedt (1930, p. 415, var. *perpusilla* (Rabh.) Grun.) includes *N. inconspicua* in *N. frustulum* (Kütz.) Grun., which itself shows similarities to *N. Hantzschiana* (see p. 100). The taxonomy of this group of small Nitzschiae is so confused that a settled determination is hardly possible at present.

Petersen's (1932*a*, p. 407) *N. Kützingiana* f. *terrestris* appears to be closely similar to some of the forms included here, and he, too, was unable to observe any striae.

The valves are linear to elliptic, the two margins being either both convex (Fig. 13 K) centrally, both flat (Fig. 13 I, J), or one flat and one convex (Fig. 13 H). They decrease more or less gradually to widely rounded, sometimes weakly cuneate apices.

The valves, to some extent, resemble those of *N. palea* in shape, but the apex is usually much more bluntly rounded, the length, which shows remarkably little variation, less, the carinal dots denser and finer and the striations never visible.

This is a common soil diatom (twenty-three samples) usually occurring with *N. palea* but in lesser numbers.

Surirella Turpin

(52) *Surirella ovata* Kütz. Fig. 18 J?, K–DD

This species is known to be very variable (Hustedt, 1930, p. 444), and the valves (6–39 μ l.; 5–8 μ br.) of the soil specimens were of two main types. On most soils the larger ones were elongate-ovoid to linear-ovoid (Fig. 18 X–Z). With decrease in length the valves become more and more broadly ovoid (Fig. 18 AA, DD). On two calcareous soils (S42, 43), the larger valves were almost isopolar (Fig. 18 O, P, U) and narrowly linear-elliptic. With decrease in length, the valves again became more and more ovoid (Fig. 18 Q–T), the smallest valves on all soils being heteropolar and ovoid. Many of the valves were weakly rostrate at the narrower end (Fig. 18 O, P, U, Y, Z). Some of the larger valves were more or less asymmetrical (Fig. 18 L, M, N, W) or irregular (Fig. 18 K, N, W), and one valve, which may belong to the species, was centrally constricted (Fig. 18 J). While the more aberrant valves were more common in cultures and enriched samples than in nature, they were by no means confined to them. Very rarely medium-sized valves were almost perfectly isopolar (Fig. 18 CC), but in girdle view all the cells were heteropolar. There were 60–90 costae in 100 μ and 20–30 striae in 10 μ.

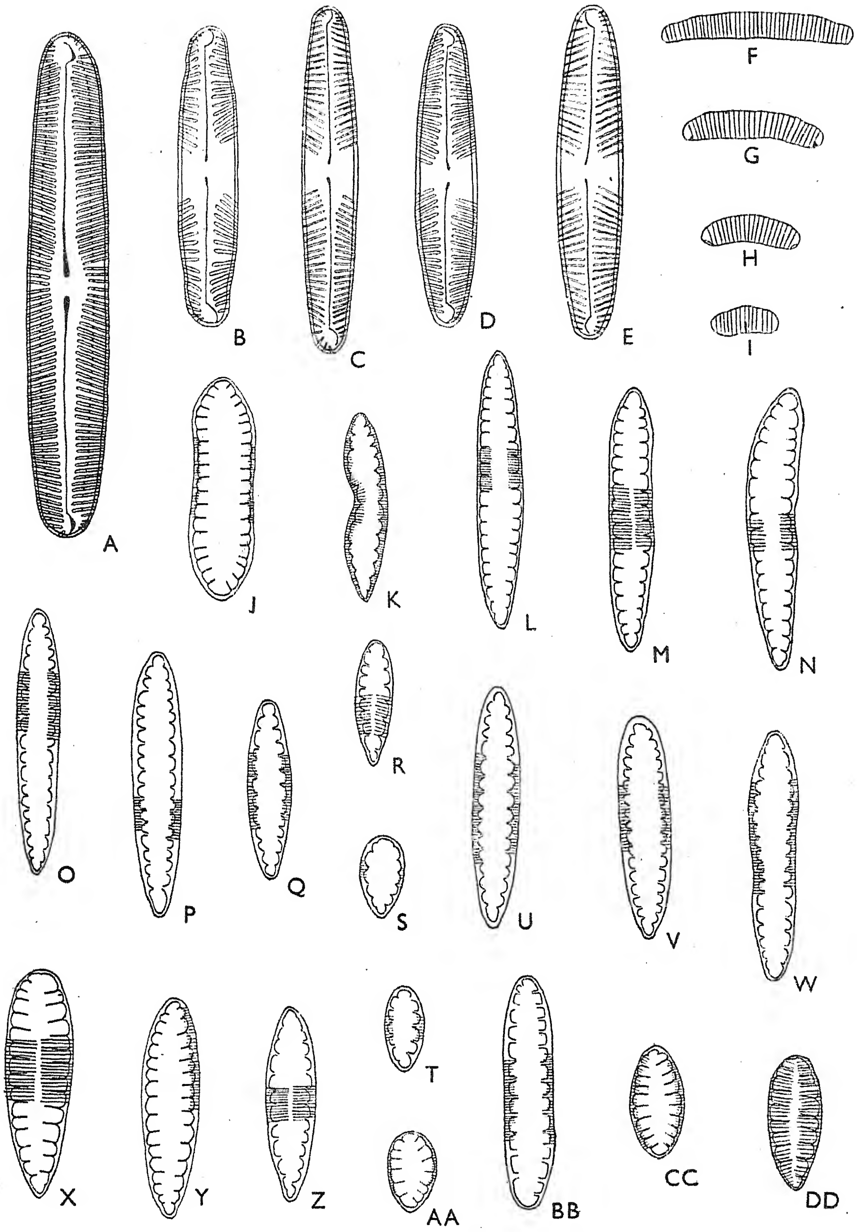

Fig. 18. A, *Pinnularia viridis* (Nitzsch.) Ehr. var. *sudetica* (Hilse) Hust.; B–E, *P. microstauron* (Ehr.) Cleve; F–G, *Eunotia tenella* (Grun.) Hust.; H, I, ?ibid.; K–DD, *Surirella ovata* Kütz.; J, *Surirella* sp. DD ×1250, rest ×1000.

The more ovoid valves are similar to those of the species in aquatic habitats (Hustedt, 1930, fig. 864) in which, and in var. *crumena* (Bréb.) Van Heurck, there may appear isopolar valves (Hustedt, 1930, figs. 863, 867). The more linear-elliptic valves resemble var. *pinnata* (W. Smith) Hust., though they are even narrower and generally have both apices pointed. As the various forms grade into one another and into the species

and varieties as described from aquatic habitats, there do not seem any grounds for separating them.

A common soil diatom (twenty-four samples), especially on well-cultivated soils, though rarely occurring in large numbers. Bristol Roach (1927, p. 576) has recorded a var. *minuta* (no authority) and another doubtful form (no description) from manured land. Recorded from Bryophytes (Hustedt, 1942).

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G. LIST OF SOILS

The figure after the description of the locality refers to the percentage of organic matter present in the top 2 cm. Soils A–I were studied less thoroughly than the others.

1. Haddington, East Lothian. Garden A. 8·8.
2. Haddington, East Lothian. Garden B. 15·7.
3. Edgbaston, Birmingham. Garden A. 13·0.
4. Edgbaston, Birmingham. Garden B. 14·5.
5. Moseley, Birmingham. Garden A. 5·9.
6. Moseley, Birmingham. Garden B. 9·1.
7. Hampden-in-Arden, Warwickshire. Edge of arable land. 8·9.
8. Haddington, East Lothian. Woodland bank. 10·3.
9. Hampden-in-Arden, Warwickshire. Edge of rabbit burrow in arable land. 5·4.
10. Gifford, East Lothian. Deciduous woodland. 5·9.
11. Woodhouse Eaves, Leicestershire. Allotment. 7.
12. Moseley, Birmingham. Well-rotted turves. 11·6.
13. Woodhouse Eaves, Leicestershire. Arable land. 5·3.
14. Malvern Hills, Worcestershire. Burnt bracken, *circa* 300 m.
15. Woodhouse Eaves, Leicestershire. Mixed woodland. 51·3.
16. Ward End, Birmingham. Park garden. 6·7.
17. Malvern Hills, Worcestershire. Path in mixed woodland. 31.
18. New Radnor, Radnorshire. Eroded bank near hedge. 4·6.
19. Moseley, Birmingham. Garden C. 15·8.
20. Beresford Dale, Derbyshire. Deciduous woodland on limestone. 14·0.
21. Manifold Valley, Derbyshire. Deciduous woodland on limestone. Sample destroyed by enemy action.
22. Radnor Forest, Radnorshire. *Vaccinium* moor, *circa* 650 m. 20·6.
23. Broadway, Gloucestershire. Woodland thicket on limestone. 14·1.
24. Bearwood, Birmingham. Garden. 11·2.
25. Longmynd, Shropshire. *Calluna* moor, *circa* 400 m. 20·0.
26. Stratford-on-Avon, Warwickshire. Mixed (mainly coniferous) woodland. 16·6.
27. Beacon Hill, Radnorshire. Moorland, *Calluna* dominant, *circa* 550 m. 26·3.
28. Bishop's Offley, Staffordshire. Hollow in arable land surrounded by deciduous trees. 4·8.
29. Leamington Spa, Warwickshire. Park garden. 10·1.

30. Edgbaston, Birmingham. Park garden. 7·6.
31. Manchester. Garden. 8·1.
32. Charnwood Forest, Leicestershire. Bare patch on bracken dominated land. 18·1.
33. Charnwood Forest, Leicestershire. Path through birch and bracken. 13·9.
34. Charnwood Forest, Leicestershire. Mixed woodland. 17·8.
35. Charnwood Forest, Leicestershire. Eroded bank on edge of oak copse. 8·9.
36. Cannock, Staffordshire. Sand heap. 3·6.
37. Stoke-on-Trent, Staffordshire. Edge of passage between houses. Much coal, fibre and mortar. 21·2.
38. Four Oaks, Warwickshire. Garden. 8·7.
39. Warley, Birmingham. Open deciduous park woodland. Soil well trodden. 37·2.
40. Warley, Birmingham. Allotment on recently ploughed grassland. Sandy. 11·0.
41. Edgbaston, Birmingham. Worn park grassland. 13·7.
42. Cotswold Hills, Gloucestershire. Garden. 9·8.
43. Cotswold Hills, Gloucestershire. Arable land, grassland for previous 50 years. 8·6.
44. Selly Oak, Birmingham. Allotment. 6·9.
45. Worcester, Worcestershire. Arable land, ryegrass and clover. 6·3.
46. Whitbarrow Scar, Westmorland. Woodland. Glacial drift on limestone. 13·3.
47. Lakeside, Lancashire. Garden. 15·9.
48. Lakeside, Lancashire. Old loam heap. 17·0.
49. Moseley, Birmingham. Garden D. 7·4.
50. Hampden-in-Arden, Warwickshire. Mixed woodland. 7·5.
51. Edington, Wiltshire. Verge of lane. Chalk soil. 9·4.
52. Winscombe, Devon. Verge of lane. Chalk soil. 22·6.
53. Foolow, Derbyshire. Garden A. 15·3.
54. Foolow, Derbyshire. Garden B. 12·1.
55. Foolow, Derbyshire. Sand heap, calcareous. 11·9.
56. Foolow, Derbyshire. Bank flanking path, calcareous. 10·4.
57. Edgbaston, Birmingham. Garden C. 12·5.
58. Moseley, Birmingham. Garden E. 7·8.

A. Winscombe, Somerset. Grass field. 30·55.
B. Wychbold, Worcestershire. Allotment. 5·7.
C. Stoke Prior, Worcestershire. Allotment A. 6·5.
D. Stoke Prior, Worcestershire. Allotment B. 6·4.
E. Caer Caradoc Hill, Shropshire. Path through scrub.
F. Birmingham. Soil from tomato boxes.
G. Newport, Shropshire. Farm path. 13 approx.
H. Scunthorpe, Lincolnshire. Edge of path. 13 approx.
I. Worcester, Worcestershire. Garden. 12 approx.

H. SUMMARY

Direct observations, supported by cultures and slides, were made on the diatoms of sixty-six soils of diverse constitution and origin. Collections, so far as possible, were made on samples under reasonably favourable physical conditions.

Rich growths only occurred on soils containing appreciable amounts of readily available phosphates and nitrates. Base-deficient soils, especially the more strongly acidic, were generally poor in diatoms and nutrients.

There was no correlation between the occurrence of the separate species and the nitrate, phosphate or potash contents of the soils, but there was a relationship between it, base deficiency, *p*H and calcium carbonate content.

Diatoms are considered to be purely surface-growing forms.

Observation on one garden soil showed no succession of species during the year. February appeared the least favourable month for growth, and summer drought reduced the flora. It is believed that, under natural conditions, there is a maximum in spring and early summer correlated with physical conditions and competition from macrophytes.

The literature concerning the size of soil diatoms is critically considered. The majority of soil diatoms belong to small-sized species, but those belonging to species reaching large size in aquatic habitats are of smaller size when present on soils. Morphologically they do not differ, apart from changes which are probably directly related to reduction in size.

The relation of size to cell shape and markings is described, with results agreeing with those of Geitler (1932). The taxonomic problems arising from changes in form with decrease in size are described.

The ecological aspect of size is reviewed, and it is considered that smallness is of biological value in facilitating apposition to the moisture films surrounding the soil particles, movement in the soil and distribution as air-borne dust. The view that the characteristic size and form of soil diatoms are the result of the chemical and physical conditions in the soil is criticized.

The diatom flora is richer than previously described. All the species possessed raphes and so the power to move.

The taxonomy, often confused, of the species is considered, seven new species and seven new varieties and forms being described. Measurements are given for all the diatoms, and their variations in form and size described and figured.

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OBSERVATIONS ON THE FLOWERING AND NECTAR SECRETION OF *RUBUS FRUTICOSUS* (AGG.)

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(With 7 figures in the text)

Introduction

Our knowledge of the secretion of nectar in plants and of the factors influencing the 'nectar flow', which is of such importance to beekeepers, is scanty. The work presented is the result of observations made on *Rubus fruticosus* (Koehleri group) (blackberry) which is a major source of nectar in some parts of Glamorgan. The general knowledge of the phenomena of nectar flow which has been obtained will, it is hoped, form a basis for further work on the subject.

The behaviour of a single plant of *R. fruticosus* was observed during the major part of its flowering period. It was one of a close association of brambles, and was isolated by cutting down its fellows. A cage of butter muslin supported on a wooden frame was erected over the plant to exclude insects. This measured $6 \times 6 \times 5$ ft., and had a removable waterproof covering for the protection of the flowers and instruments during wet weather: it was placed over the plant the day the first flowers opened.

Meteorological observations

A soil thermometer was sunk to a depth of $12\frac{1}{2}$ in., 6 in. from the stem of the plant. The air temperature was measured at a height of 2 ft., which was the height of the blossoms. An evaporimeter and hair hygrometer were placed on a wooden stand just above blossom level. Readings were taken at 1 hr. intervals, and the general weather conditions were also noted at the same time. Weather conditions at night were noted in general terms.

Description of plant

The plant possessed one main shoot about 20 ft. in length. This was docked to a length of 6 ft., as the terminal portion had lain across a path and was badly damaged. It bore twelve well-grown lateral shoots and one aborted stump. The former were numbered 1–12: each bore a terminal cluster of flowers. In the axil of shoots 1, 2 and 3, and also in the axil of the aborted shoot, axillary shoots had developed. These were numbered A, B, C and D. A and B were well grown and bore five and four clusters of flowers, respectively. C and D were weak, D bearing a small terminal cluster of flowers. C died during the observation period. The shoots differed considerably in stoutness, and at the close of the flowering period sections were cut at comparable levels across each stem and the diameter recorded.

Course of observations

Observations began on 19 June when the first flowers opened and finished on 13 July. Owing to the discovery of a possible source of error, the nectar samples from 19 to 29 June had to be discarded. The flowers were examined morning and evening, i.e. at

approximately 12 hr. intervals throughout their lives. The morning work began between 5.0 and 7.0 a.m. (G.M.T.), and the evening between 5.0 and 7.0 p.m. At the height of the flowering, the sampling took up to 3 hr. (morning and evening), but as the shoots were sampled in strict rotation, the 12 hr. period was fairly well maintained.

The flowers were numbered in order of opening and their position on the shoot recorded. The positions of the petals and stamens were noted and dehiscence of the anthers recorded when it occurred. The size of the flowers, i.e. the petal span, was recorded in some cases. The time at which each flower was examined was noted.

Nectar sampling

This was accomplished by means of 5–6 mm. glass tubing drawn out into slender capillaries, 0·5–1 mm. in bore. A rubber teat was fixed to the broad end of the tubing. The nectar was withdrawn by slightly exhausting the teat and applying the capillary tip to the surface of the nectary, when the nectar ran up into the capillary. Several tappings were made around the nectar disk to ensure that all the nectar was removed. The nectar was withdrawn well up into the capillary, and the tip sealed immediately in a flame. The samples were then transferred indoors, and the broad end of the tube sealed with cotton-wool soaked in melted beeswax. The samples were then stored at 3° C. until they were analysed.

Estimation of sugar in the nectar samples

The volume of the nectar sample was measured by transferring the liquid from the capillary to an opsonic pipette. The sugar percentage, estimated as cane sugar, was then found by the use of an Abbé refractometer. A small quantity of distilled water was drawn up into the capillary in order to rinse off any remaining traces of nectar. The volume of the liquid was measured and its sugar content estimated. The sum of these two estimations was taken and expressed as milligrams of sugar. A second rinsing of the sample tube was found to be unnecessary as no appreciable amount of sugar remained.

Results

General biology

On all shoots the terminal flower opened first and was the longest lived. The next flowers to bloom were the terminal buds on each of the lateral branches of the inflorescence. These were designated 'terminal' flowers. Their average life, calculated from 134 blooms, was 90 hr. When the terminal flowers of a shoot finished blooming, there was generally a lapse of 1–2 days before the 'subterminal' flowers (i.e. all flowers other than terminal flowers) commenced to bloom. The life of the subterminal flower was considerably shorter, the average for eighty-nine blooms being 60 hr.

Nectar secretion duration

Nectar secretion began just before the petals started to unfold, and finished when the petals had fallen and the filaments of the dehisced stamens were beginning to incurl over the carpels.

Amount of nectar secretion

The blackberry has a relatively shallow nectar cup, and the volume of the nectar is affected by changes in relative humidity. It was hoped at the beginning of observations

to assess both the volume and the sugar content of each sample, but as some shrinkage in volume took place while the samples were in store awaiting analysis, the sugar content alone was determined.

The amount of sugar secreted by individual flowers varied widely. Flower 1 of shoot 1 yielded 19·5 mg., while flower 4 of shoot B4 yielded only 3·7 mg. These examples illustrate extremes of a rule that will be demonstrated later, namely, that the diameter of

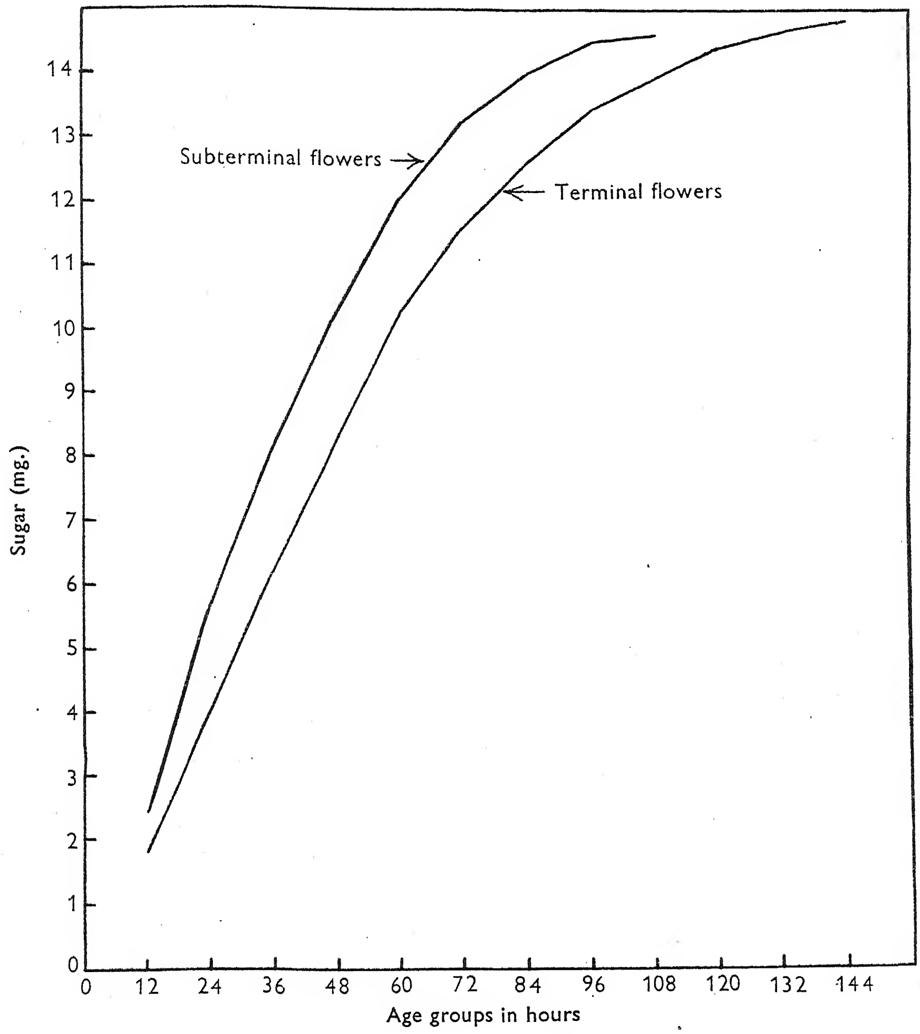

Fig. 1. Total sugar secretion curves of terminal and subterminal flowers on stems 2·9–4·6 mm. in diameter.

the shoot which bears the flower bears a positive relation to the amount of sugar secreted by the flower. Shoot 1 was the most robust shoot on the plant, shoot B4 the weakest.

Fig. 1 shows, as progress curves, the average total secretion of sugar from terminal and subterminal flowers on stems 2·9–4·6 mm. in diameter for the period from 29 June to 5 July. The average value was taken to minimize any possible effect of weather or other conditions which might influence separate graphs.

In the graph of the terminal flowers, secretion is maintained at a high level for the first 3 days of the flower's life, and then falls off fairly rapidly. About three-quarters of the total amount of sugar is secreted in the 3-day period, an average of 11·5 mg.

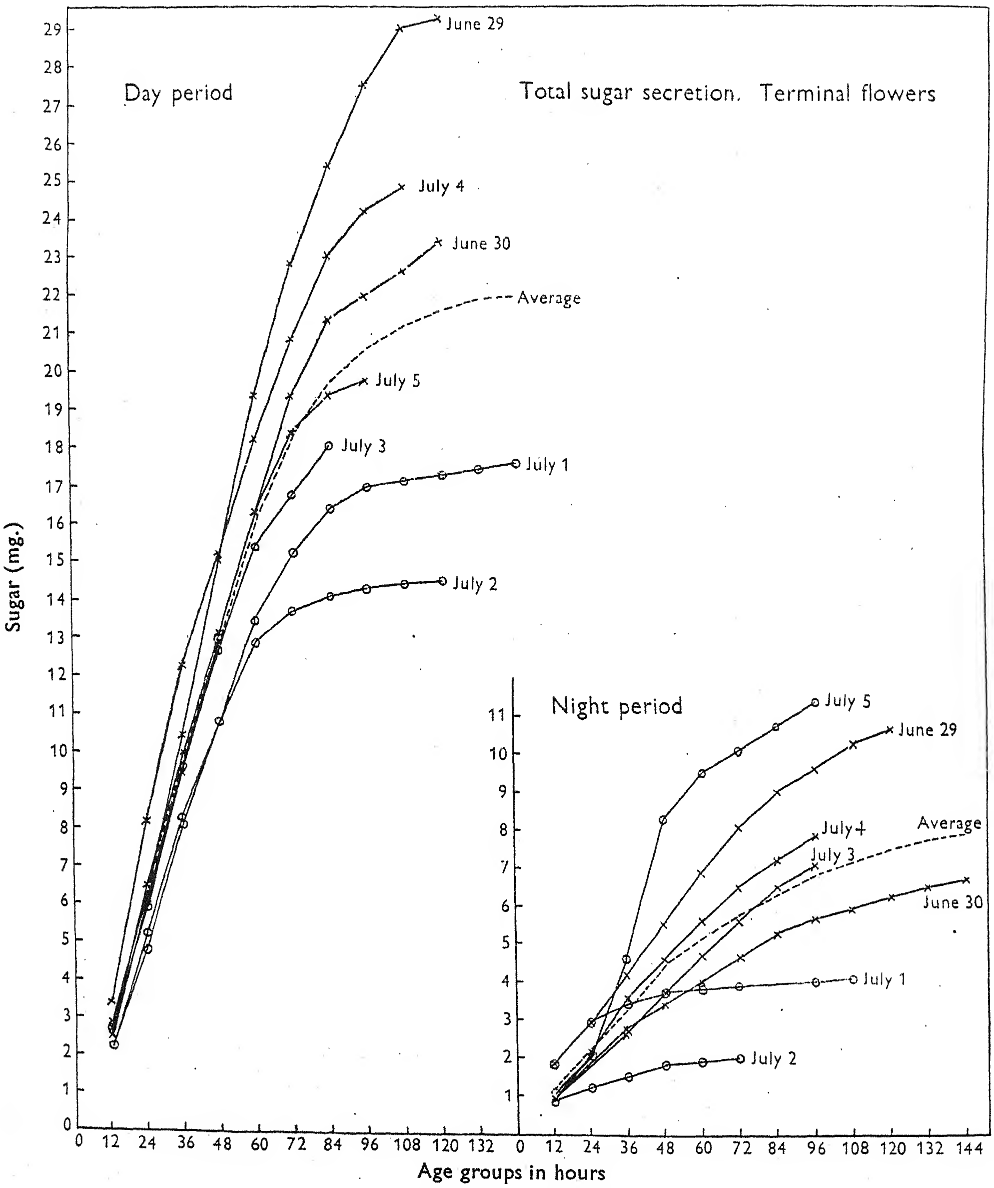

Fig. 2. Total sugar secretion curves for terminal flowers for day and night periods from 29 June to 5 July.

The total amount secreted by subterminal flowers reaches on average approximately the same figure as that of the terminal flowers, 14·6 mg. The life of the subterminal flowers is much shorter than that of the terminal flowers. The graph shows a steeper climb in consequence with bigger daily average secretion.

It is probable that the terminal flowers secrete more sugar than the subterminal: the reason why the two classes show the same total figure in Fig. 1 will be explained in the discussion of the results.

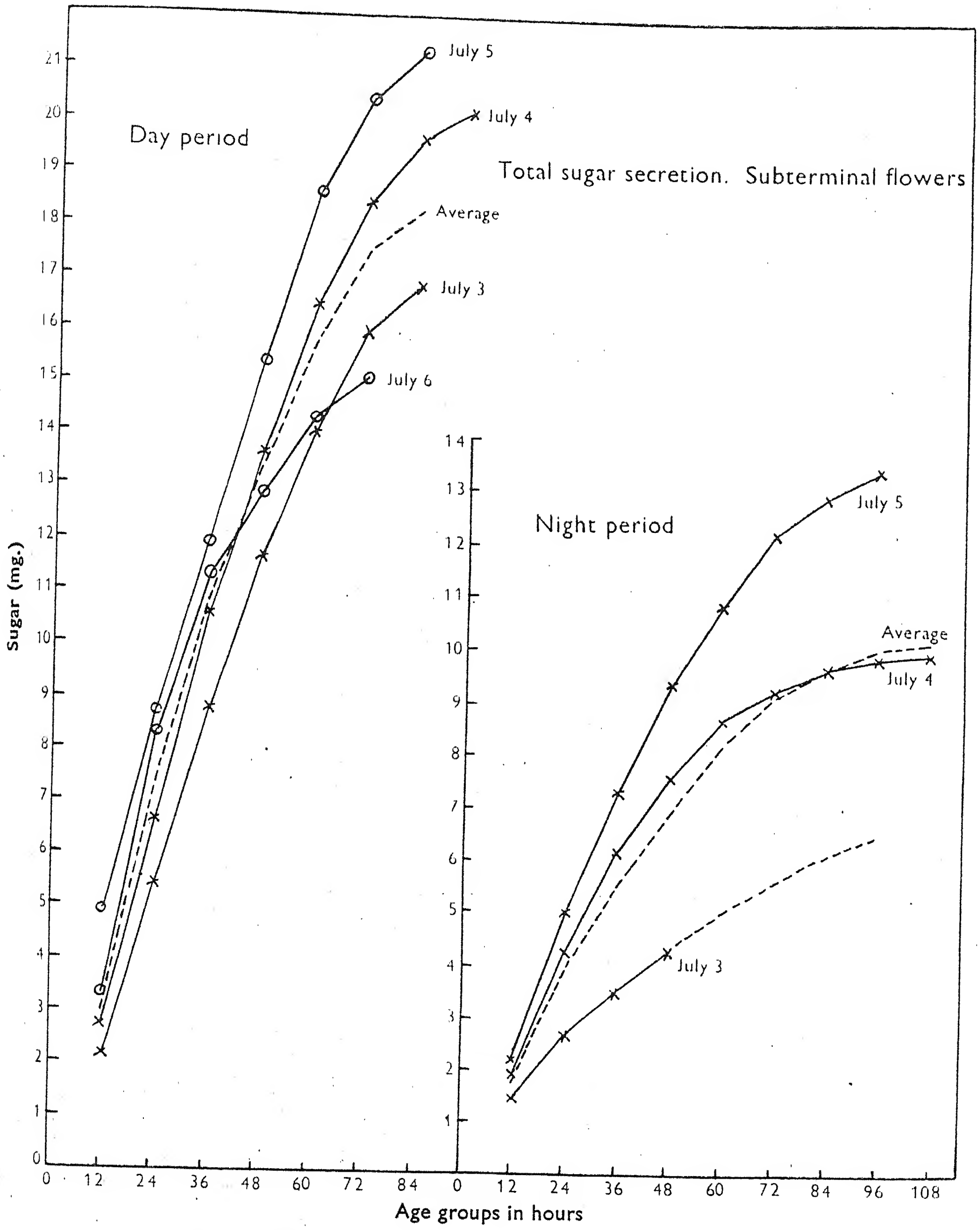

Fig. 3. Total sugar secretion curves for subterminal flowers for day and night periods from 3 to 6 July.

Day and night secretion of sugar

There is a marked diurnal rhythm in the amount of sugar secreted. Most of it is secreted during the day period; the amount of sugar in the nectar collected in the early

mornings is very small. This does not mean that the volume of nectar is small. After a very humid night the volume may be as large as that collected in the evening period. An occasional flower will secrete heavily during the night, but this is unusual enough to evoke comment. For example, on the night of 1 July one flower secreted 6·2 mg., and on the previous night one secreted 4·4 mg. The average secretion of flowers in the same age class (excluding these two) was 0·4 and 1 mg. respectively.

The amount of sugar secreted during the day and night periods can be assessed from Figs. 2 and 3. These were constructed by plotting the average secretion of sugar in milligrams for each age class as a cumulative graph. This was done separately for each day and night. Then the average values of these separate curves were plotted to give an average total secretion graph for the day and night periods. The terminal and subterminal flower graphs were plotted separately.

The total day secretion graph of the terminal flower reaches the figure of 22 mg. of sugar, as against the night secretion of 8 mg. of sugar. Therefore the ratio is about 3 : 1. The subterminal flower graphs are rather different. The totals for day and night secretion average 16 and 10 mg. respectively, a ratio of 1·6 : 1.

The sugar secretion and age of flower

The rate of secretion of sugar varies with the age of the flower. This is illustrated in the progress curves of Figs. 1–3, and by the rate curves of Fig. 4. Here the average amount of sugar secreted by each class of flower during the period 29 June–5 July is given. The data for terminal and subterminal flowers are separated, but all flowers were borne on shoots 2·9–4·6 mm. in diameter.

The curve of day secretion obtained for terminal flowers shows that the major part of the sugar is secreted in the first 60 hr. of the flower's life, then the secretion falls off rapidly, but continues right to the end of the flower's life. The night secretion curve is of a similar shape, although the values recorded are much lower than those of the day period. The curves for the subterminal flowers are substantially similar, but show a decided maximum at the age of 24 hr. This is apparent in both the day and night secretion curves. The values at 12 and 24 hr. are greater than those recorded for the terminal flowers. The difference in the length of life of these two flower classes can be seen at a glance from these curves.

Daily rhythm of secretion throughout the blooming period of the flower

In order to obtain a more detailed record of daily secretion, six flowers were exploited for nectar at 2 hr. intervals throughout the day periods of their lives. The flowers were 'prepared' early each morning by withdrawing the bulk nectar in a pipette, and then drying the surface of the nectary by touching it with filter paper. Then 2 hr. were allowed to elapse before the sample was taken. The amount of nectar secreted in 2 hr. periods is too small to be collected in a pipette. Instead, strips of filter paper, 2 mm. wide, were inserted in the nectar cup, and the amount of paper wetted gave an arbitrary figure, by which the amount of secretion could be measured. Precautions were taken to ensure the even wetting of the paper.

Detailed notes of movements of flower parts were taken throughout.

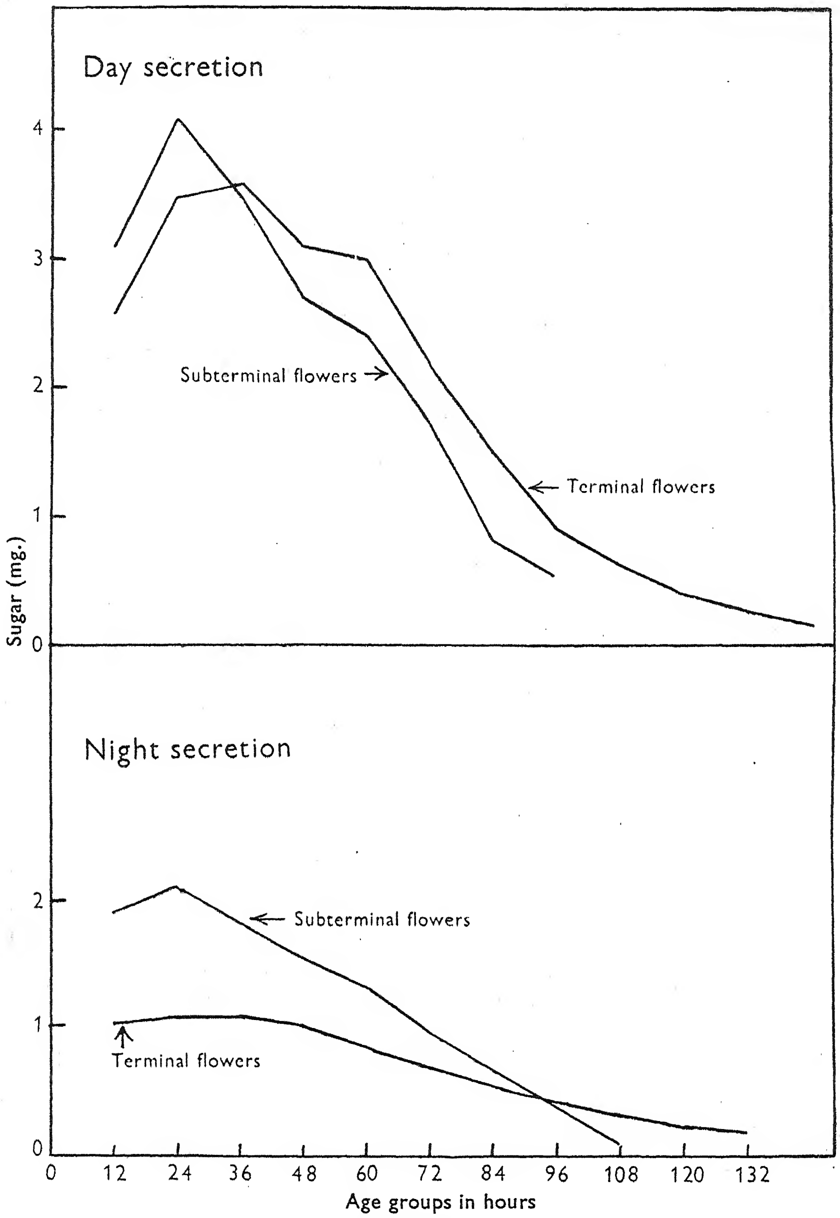

Fig. 4. Graphs showing amount of sugar secreted by flowers of different ages for day and night periods.

Consideration of results

Summarizing the results we find that nectar secretion is maintained at a high level during the day the flower opens. This coincides with a period of rapid expansion and movement of the flower parts. On the second day secretion is very steady, decreasing towards the evening. After the opening movement the flower shows very little change on this day. On the third day of the flower's life no nectar is found until a reflexion of

the petals takes place. The secretion is thereafter continuous throughout the day, reaching at 12.30 p.m. a maximum value which is half the figure of the first day. The secretion ceases as the stamens incurl over the carpels. It is seen, therefore, that nectar secretion coincides with the period of flower 'blooming', and although no direct relationship may be claimed between flower growth and movement and nectar secretion, there is a certain degree of correlation between the three phenomena. (Flower growth and movement are spoken of separately, for it has not yet been determined whether the movements are due to turgor changes or to differential growth.) It has been demonstrated that there is very little sugar secreted during the night period, and flower movement does not take place during the night. When the opening movement of the flower has occurred during the morning, then nectar is found in the cups; this is clearly seen in the secretion graph for 12 July (Fig. 5). This graph is useful because it shows the behaviour of flowers in

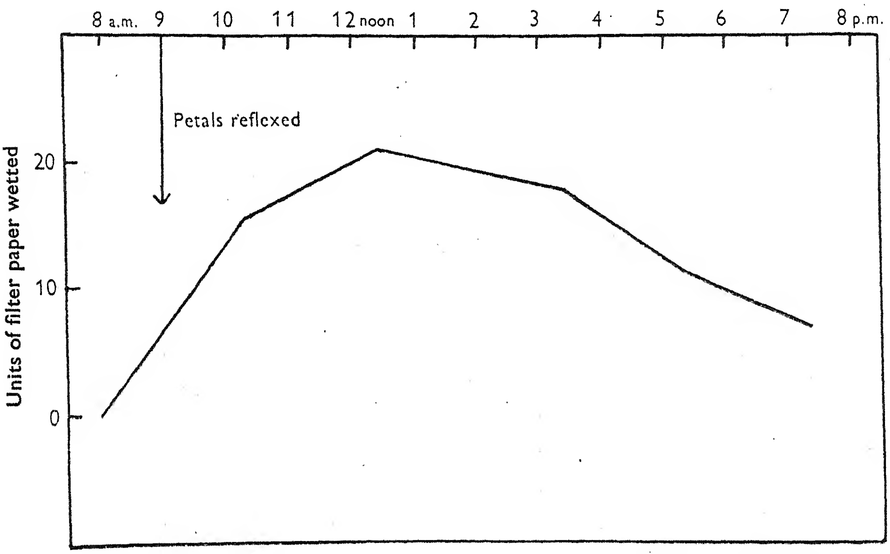

Fig. 5. Average secretion graph of five flowers during the third day of blooming. The opening movement (a reflexion of the petals) occurs between 8 and 10 a.m.

which obvious expansive growth has ceased—that is, the flowers are 'full blown' and for this reason we can separate the two phenomena of growth and movement. It appears likely that the same 'stimulus' which causes the opening movement of the flower also stimulates the exudation of nectar from the nectary. Should the reflexion of the petals (and the other flower movements) prove to be due to growth, then the secretion of nectar takes place whenever growth takes place in the flower, and as long as growth continues. Moreover, the amount of nectar secreted follows the growth rhythm of the flower, being greater when growth is rapid (during the first day of blooming) and lower when growth is almost completed (second and third day of blooming).

Sugar secretion and shoot diameter

The diameter of the shoots bearing the flower trusses varied considerably. The measurements are given in Table 1. It was thought that the flowers borne on the more robust shoots would secrete more sugar than those on the thinner shoots. This was

found generally to be the case (see Table 2) for both terminal and subterminal flowers. There are certain anomalies: for instance, the subterminal flowers of shoot 1—the stoutest shoot—show a smaller average secretion than those of B 1, which is more slender. As these averages were based on flowers open on different days and might be subject to differences on that account, a more exact basis of comparison was sought. The average secretion of flowers of the same age, open on the same day, was compared in shoots of different sizes. In order to assemble enough data for this, the shoots were grouped into three series (see Table 1). Shoot 1 was so much stouter than the rest that its data comprised series 1. The division into series 4 and 6 is arbitrary. Shoot B4 (2·1 mm. diameter) had so few flowers that it could not profitably be compared with the others. Table 3 shows the result of the arrangement. In almost every instance the average secretion of the flowers of shoot 1 exceeds that of series 4, which in its turn exceeds that of series 6. The average amount by which secretion in series 4 exceeds that in series 6 is 0·5 mg. for terminal flowers, and 1·1 mg. for subterminal flowers.

Table 1

Shoot	Diameter in mm.	Series	Shoot	Diameter in mm.	Series
1	5·8	S1	6	3·5	S6
2	4·6	S4	B3	3·5	
7	4·5		A4	3·4	
4	4·2		8	3·3	
12	4·2		A5	3·3	
11	4·1		A3	3·1	
B1	4·0		A2	3·0	
5	3·9		D1	2·9	
9	3·8		B4	2·1	
10	3·8				
B2	3·8				
3	3·6				

Table 2. *Average amount of nectar secreted per flower compared with diameter of shoot*

Shoot	Diam. of shoot in mm.	No. of flowers in sample	Average total secretion in mg.
	Terminal flowers		
1	5·8	15	15·4 ± 3·3
3	3·6	12	13·2 ± 2·8
2	4·6	9	12·5 ± 3·5
B2	3·8	10	11·8 ± 1·1
A3	3·1	10	9·9 ± 1·8
A2	3·0	8	8·6 ± 1·3
B4	2·1	3	5·6 ± 0·7
	Subterminal flowers		
7	4·5	6	13·0 ± 2·1
4	4·3	18	12·8 ± 1·9
2	4·6	4	12·6 ± 1·6
5	3·9	8	12·4 ± 2·0
B1	4·0	19	11·9 ± 2·0
1	5·8	3	10·2 ± 0·1
B3	3·5	4	9·9 ± 1·2
A5	3·3	11	8·7 ± 1·8
A4	3·4	3	8·3 ± 0·4

Table 3. *Detailed comparison of amount of nectar secreted per flower with shoot diameter*

Date period	Day or night	Age classes of flowers in hr.	Mean of averages in mg. of sugar		
			S1	S4	S6
29 June	Day	1–12, 24–36, 36–48 and 96–108	—	3·6 ± 0·9	2·9 ± 0·7
30 June	,,	1–12, 48–60, 60–72	—	3·2 ± 0·7	2·7 ± 0·5
30 June	,,	24–36	5·5 ± 0·3	—	3·1 ± 0·3
1 July	,,	24–36, 48–60, 72–84 and 84–96	—	2·1 ± 0·9	1·8 ± 0·5
1 July	,,	48–60	4·8 ± 0·9	3·1 ± 1·5	2·4 ± 0·6
1 July	,,	1–12, 48–60	4·1 ± 0·8	2·8 ± 1·4	—
2 July	,,	48–60	—	2·0 ± 1·3	2·3 ± 0·5
2 July	,,	1–12, 24–36	3·6 ± 0·8	2·7 ± 0·6	—
2 July	,,	72–84	0·7 ± 0·6	—	0·2 ± 0·1
29 June	Night	12–24	1·5 ± 0·5	—	0·9 ± 0·2
30 June	,,	24–36	0·8 ± 0·1	—	0·4 ± 0·1
1 July	,,	12–24	0·7 ± 0·05	1·1 ± 0·3	—
1 July	,,	60–72	0·3 ± 0·2	—	0·16 ± 0·09
2 July	,,	12–24, 36–48	0·5 ± 0·1	0·5 ± 0·2	—
6 July	Day	1–12, 12–24, 24–36	—	4·5 ± 1·0	2·9 ± 0·9
5 July	,,	1–12	—	4·3 ± 1·8	3·5 ± 1·0
4 July	,,	1–12, 24–36	—	3·8 ± 1·0	2·8 ± 0·5

Variation in amount of sugar secreted from day to day

The total secretion curves of day and night for different dates show decided differences. To take an extreme case, the curve for 2 July shows the sugar secreted (for flowers in all age classes) on that day to be only half the amount secreted on 29 June. This indicates some factorial influence. Furthermore, if the curves are arranged according to their dates it is seen that the 29th > 30th > 1st > 2nd < 3rd < 4th < 5th. This sequence is exhibited alike by the terminal and the subterminal flower curves (excepting that in the former the figure for 4 July exceeds that of 5 July), and is depicted in Fig. 6 by plotting the value of the total secretion curve at 84 hr. age against the date.

Again, if the curves of night secretion of terminal and subterminal flowers are arranged according to their dates it is seen that 29th > 30th > 1st > 2nd < 3rd < 4th < 5th. In Fig. 6 the meteorological and general biological data are arranged about these curves.

The meteorological data refer to the day conditions only, that is those recorded between 5.0 a.m.–9.0 p.m. G.M.T. The biological data include the total number of flowers in bloom and also the total number of young flowers (1–48 hr. old) in bloom on the various dates. Fig. 7 shows the relative proportions of terminal and subterminal flowers which go to the make-up of the total flower graph.

Factors influencing nectar secretion

Examination of the data so displayed shows that the curve of average nectar production per flower follows very closely that of the total number of flowers in bloom and even more closely that of the young flower curve. That is to say, on days when a large number of flowers is in bloom, the average secretion of the flowers is higher. When a relatively small number of flowers is out, the average secretion per bloom is lower. So the biological data are linked. It is unfortunate that the data of the nectar secretion during the early period of blooming of the terminal flowers (20–28 June) are not available, for if, as appears likely, greater average secretion goes hand in hand with a peak in the

blooming, the terminal flowers should show a greater average secretion per bloom than the subterminal flowers. It is seen that the average secretion for these two types is equal in amount. This is believed to be true only for the 'waning' period of terminal flower blooming and the 'waxing' period of subterminal flower blooming which were the periods from which the graphs were compiled.

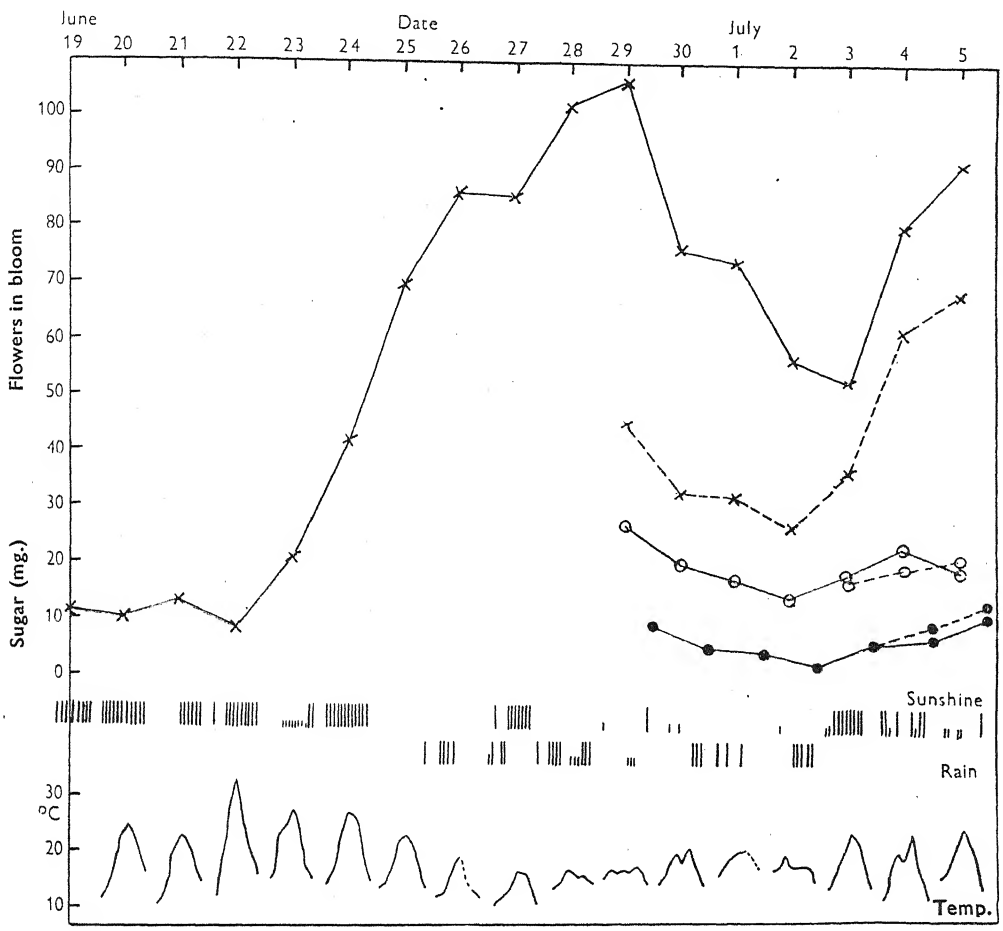

Fig. 6. Composite figure of biological and meteorological data. Total number of flowers in bloom (×——×). Number of flowers 1–48 hr. old (×----×). Total nectar secretion in milligrams of sugar of (*a*) terminal flowers, day period (⊙——⊙), night period (●——●); (*b*) subterminal flowers, day period (⊙----⊙), night period (●----●). Sunshine and rain records: each full stroke equals 1 hr. of sunshine or rain. A half-stroke indicates partly cloudy conditions on sunshine record and drizzle on rain record.

The meteorological data seem to show but little correlation with the sugar secretion. The highest average per flower was obtained on 29 June, a dull, still, cool day, and the lowest average secretion was obtained on 2 July, which was also dull, still and cool.

It seems that a sunny period precedes the first burst of flowering and is coincident with the second. It seems that the average nectar secretion falls with a succession of sunless, rainy days, and rises with a succession of sunny days, but this may be an effect of the speeding up of the flower opening on a sunny day, and the slowing down on a

dull day. The lower average secretion on 5 July, when the weather was still warm and sunny, indicates the independence of nectar flow and immediate external environmental conditions. Another example illustrating this independence is seen if one compares 1 and 3 July. The weather on 1 July was rainy and mild, and on 3 July warm and sunny, yet on both days the amount of sugar secreted was the same.

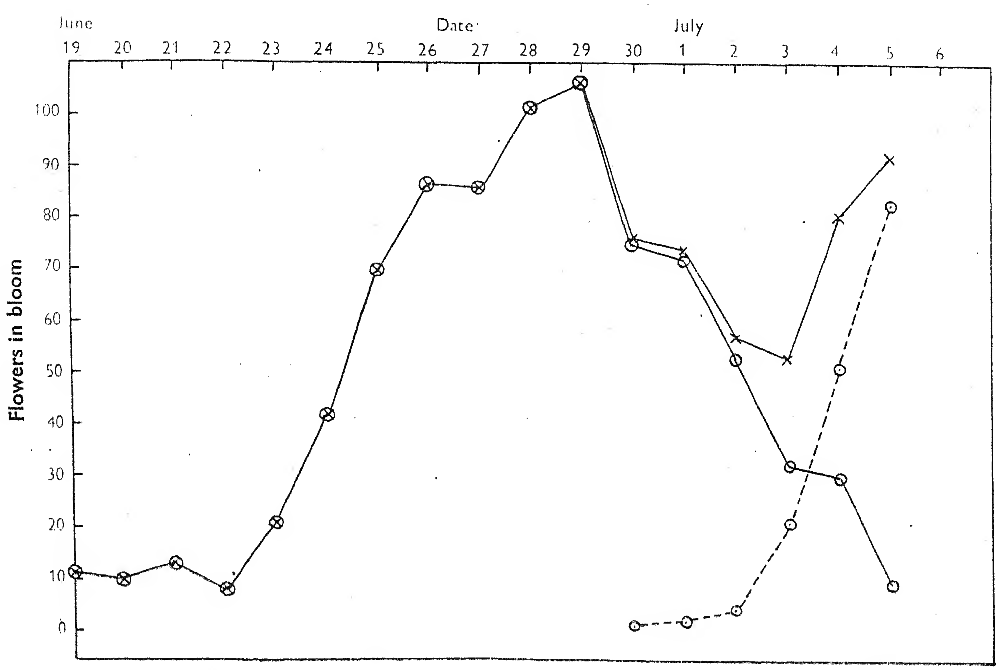

Fig. 7. Graph showing proportions of terminal (⊖——⊖) and subterminal (⊙----⊙) flowers included in total number of flowers (×——×) in bloom from 19 June to 5 July.

Conclusions

It is not, therefore, possible to arrive at any definite conclusions on the factors influencing nectar flow in the blackberry from the data presented. The weather conditions prevailing at the time of flowering seem to have little effect on the amount of sugar secreted. However, during the course of the observations, the external conditions were relatively equable, so all that may be said is that they were not limiting factors. There seems to be a 'natural' rhythm of flow which follows the rhythm of blooming. The causes of these rhythms are unexplained. An investigation into the early history and experiences of the flowering shoot seems essential before further knowledge is gained.

Summary

1. Observations on the biology and nectar secretion of flowers of *Rubus fruticosus* were made during a major part of the blooming period.

2. 'Terminal' flowers have an average life of 90 hr. as against 60 hr. for 'subterminal' flowers.

3. There are two peaks in the blooming due to the opening of the terminal and subterminal flowers respectively.

4. The average amount of sugar secreted by terminal flowers (peak of blooming period to close) and by subterminal flowers (beginning to peak of blooming period) is approximately equal, i.e. 14·5 mg.

5. The amount of sugar (estimated as cane sugar) secreted per flower varied from 19·5 to 3·7 mg.

6. Nectar secretion is coincident with growth and movement of the flower parts. It begins when the petals begin to unfold and continues until the filaments of the stamens incurl over the carpels after petal fall.

7. Secretion varies in amount with the age of the flower.

8. There is a diurnal rhythm in sugar secretion, the ratio of day to night being 3 : 1 for terminal flowers and 1·6 : 1 for subterminal flowers.

9. Flowers borne on stouter shoots secrete more nectar than those borne on thinner shoots.

10. A peak in the blooming is accompanied by a higher average secretion of nectar per flower.

11. Weather conditions at the time of blooming have no obvious effect on nectar secretion.

THE OCCURRENCE OF A NUT OF *TRAPA NATANS* L. IN THE OUTER HEBRIDES, WITH SOME ACCOUNT OF THE PEAT BOGS ADJOINING THE LOCH IN WHICH THE DISCOVERY WAS MADE

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(With 2 figures in the text)

Introduction

For a number of years, expeditions organized by the Department of Botany, King's College, Newcastle upon Tyne, have been investigating the flora and fauna of the Inner and Outer Hebrides. During the course of this work, a number of plants new to, or rare in, the British Isles have been detected. Amongst these were American forms like *Naias flexilis* Rostk. and *Spiranthes stricta* Nelson, Arctic-Alpine species such as *Carex capitata* L., *C. bicolor* All., *C. glacialis* Mack., *Erigeron uniflorus* L. and others, like *Illecebrum verticillatum* L., *Juncus capitatus* Weig, and *Cicendia pusilla* Griseb., only previously recorded from far-distant stations. To the latter may now be added *Trapa natans* L., although the material collected is not of recent origin. A single nut was found entangled in a dense mass of *Potamogeton pectinatus* L. debris washed up on the south-east shore of Loch Ceann a' Bhaigh, on South Uist, in the summer of 1944. A careful examination of the fruit soon revealed the fact that it was not a living specimen, but that it must have been washed out of peat deposits somewhere in the vicinity of the intricate system of lochs and lochans of which Loch Ceann a' Bhaigh forms the lowest member.

The nut was in perfect condition, and agreed in type with the var. *coronata* Nath. as described and figured by Schroeter (1899). However, it was more slender and possessed more acuminate spines than the example figured. It resembled, rather closely, one illustrated (fig. 188) by Gunnar Andersson (1898) from a peat bed in Finland.

Trapa natans has not been known to occur in Britain since the Ice Age, although it has been listed from the Cromer Forest Bed by Reid (1899). Still, the present discovery, although important, is not very astonishing, as remains of the plant have been reported in post-glacial peats in Norway, Denmark, etc. (Gams, 1926), in areas beyond the present European range of plant. From the facts outlined above it will be clear that the exact source whence the nut was derived is unknown, but, very fortunately, careful scraping of its surface yielded enough peat to provide a count of 140 tree-pollen grains. Furthermore, during the 1939 expedition, several peat cuttings had been examined in the general neighbourhood, and samples taken for pollen determinations. Material was therefore available for attempts to discover the source and relative age of the specimen.

Three of these peats have been examined, and two are reported on in detail. The first, about 2 m. in depth, was collected on the shores of Calvay Island, lying at the

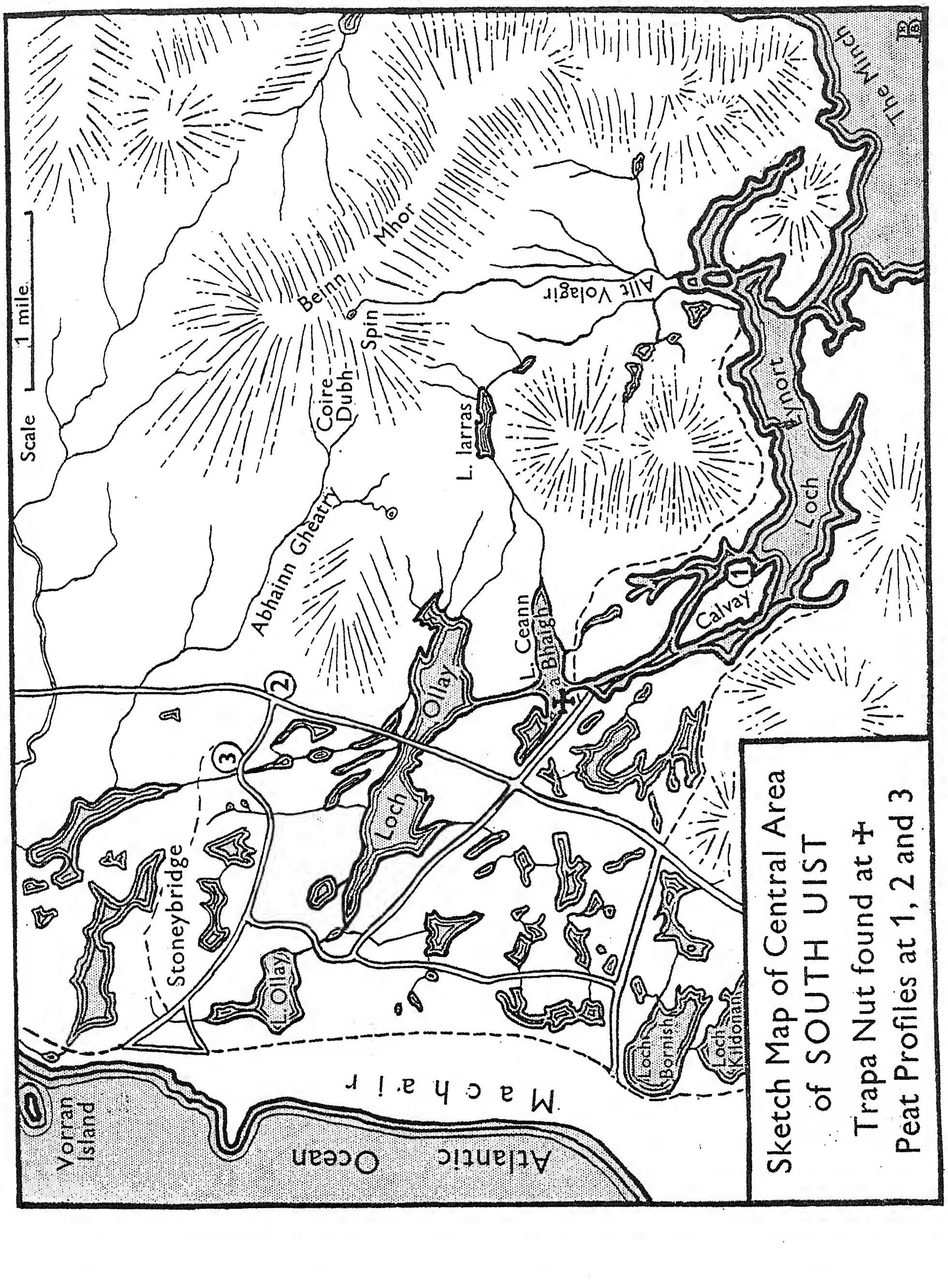
Sketch Map of Central Area of SOUTH UIST
Trapa Nut found at ✝
Peat Profiles at 1, 2 and 3
Scale
1 mile
Beinn Mhor
Coire Dubh
Spin
Allt Volagir
L. Iarras
Abhainn Gheatry
L. Ceann a Bhaigh
Loch Ollay
Loch Eynort
Calvay
Stoneybridge
L. Ollay
Loch Bornish
Loch Kildonan
Machair
Atlantic Ocean
Vorran Island
The Minch

Fig. 1.

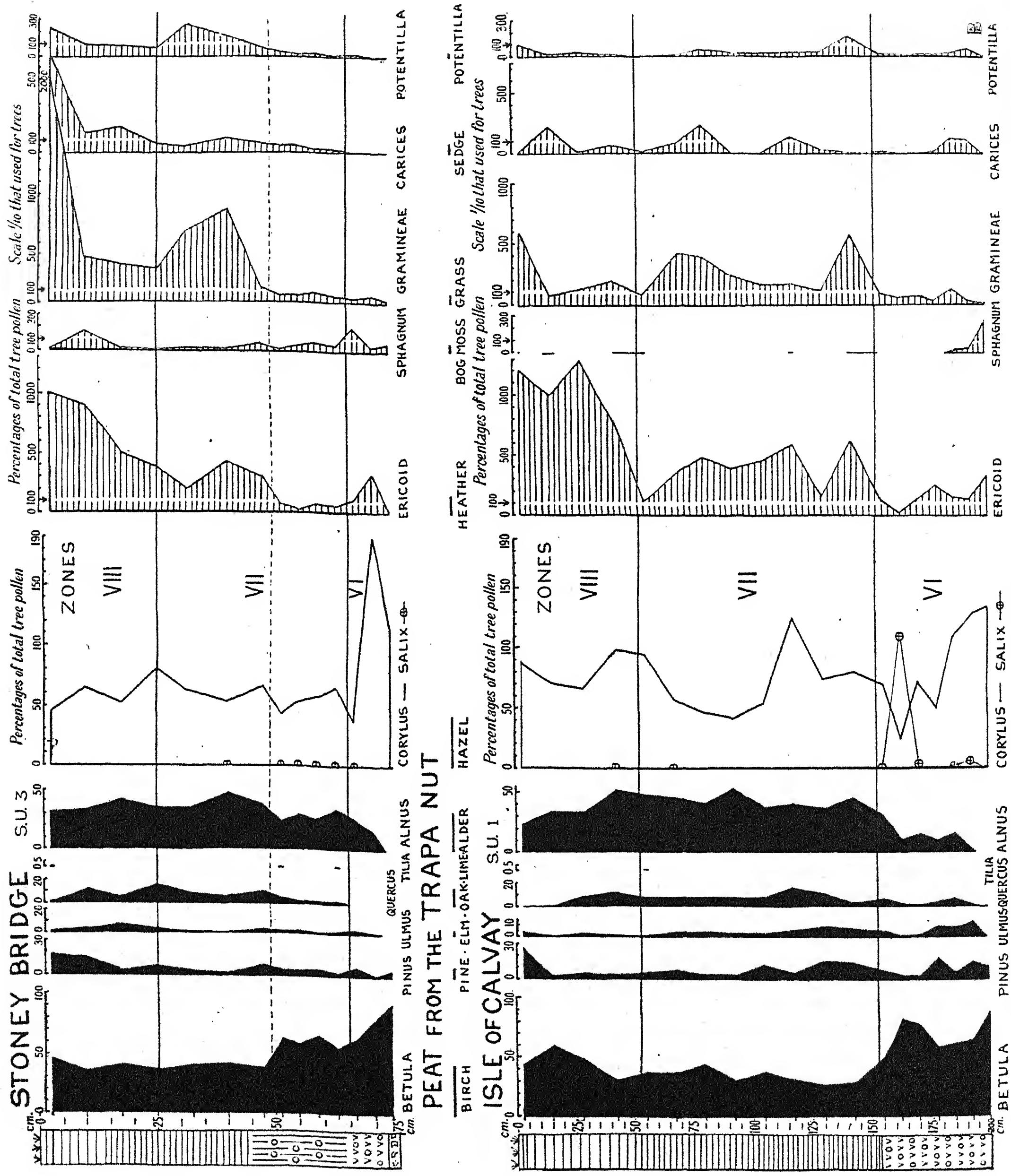
STONEY BRIDGE
S.U. 3
BETULA
PINUS ULMUS
QUERCUS
TILIA ALNUS
ZONES
VIII
VII
VI
Percentages of total tree pollen
CORYLUS — SALIX
ERICOID
SPHAGNUM
GRAMINEAE
CARICES
POTENTILLA
Scale 1/10 that used for trees
PEAT FROM THE TRAPA NUT
ISLE OF CALVAY
S.U. 1
BIRCH
PINE · ELM · OAK · LIME · ALDER
HAZEL
HEATHER
BOG MOSS
GRASS
SEDGE
cm.

Fig. 2.

head of Loch Eynort, the sea loch into which Loch Ceann a' Bhaigh flows. The base of this peat was not far above the low-tide limit. The other two were obtained near the Stoneybridge road, not far from Loch an Àthain, a little above 50 ft. O.D. These peats were only $\frac{3}{4}$ m. deep, but investigations tend to indicate that they were being deposited during the same period as the Calvay sample. Of these peats the first occurs to the south-east, and the other two to the north-west, of the *Trapa* locality; all three therefore lie in close proximity to the complicated system of lochs beginning at Loch Ollay in the north-west in the machair zone, as well as at Loch Iarras in the north-east, on the moorlands, and ending in the brackish Loch Ceann a' Bhaigh and Loch Eynort.

In addition to examining the peats, the present surface vegetation was listed with the following result:

Potentilla erecta	f.	*Eleocharis multicaulis*	f.
Drosera rotundifolia	f.	*Scirpus caespitosus*	dom.
D. anglica	o.	*Rhynchospora alba*	l.a.
Scabiosa succisa	f.	*Schoenus nigricans*	f.
Calluna vulgaris	a.	*Carex stellulata*	f.
Erica cinerea	l.a.	*C. Goodenowii*	o.
E. Tetralix	l.a.	*C. panicea*	o.
Anagallis tenella	f.	*C. flava*	o.
Pedicularis sylvatica	a.	*C. binervis*	o.
Pinguicula vulgaris	o.	*Agrostis canina*	f.
Salix atrocinerea	(loch edge)	*Molinea caerulea*	f.
Orchis ericetorum	o.	*Festuca vivipara*	o.
Narthecium ossifragum	f.	*Sieglingia decumbens*	f.
Juncus squarrosus.	o.		

Amongst the mosses, the predominant species were *Sphagnum* spp., *Hypnum Schreberi*, *Brachythecium undulatum*, *Hylocomnium splendens*, *H. loreum*, *Thuidium tamariscinum* and, near the *Salix*, *Myurium hebridarum.*

Peat deposits

Previous work

Up to the present, but little work has been done on the Outer Hebridean peats. Lewis (1906) studied some from North Uist, where blanket peat is extensive. In those from lower levels, he found characteristically at the base, a hard black layer with birch bark differentiated from three overlying layers, respectively noted as containing birch twigs, *Phragmites* and a *Scirpus-Eriophorum* peat. In Skye, likewise, he observed that the basal layers consisted of birch, but on the Isle of Lewis he reported Arctic plants beneath the birch (Lewis, 1907).

Samuelsson (1910) re-examined the peats on the Isle of Lewis, and in one, lying just south of Barvas, he found two birch-forest layers with *Eriophorum vaginatum* peat between. The lowest lay on moraine debris, and he identified it as constituting the Lower Forest zone of Geikie (1894). Incidentally, he cast unnecessary doubt on Lewis's idea that the single bottom bed was lower forest.

Erdtman (1924) examined a series of Scottish mosses from the standpoint of pollen statistics; amongst them were groups from Skye and Lewis. He discovered that the lower layers showed very high figures for birch, usually accompanied by a hazel maximum and no alder, although a subsequent rapid increase in the latter occurred. These results are expressed in more familiar terms by Fraser (1943) when he writes that peat

formation in Scotland in general began at the period of the hazel maximum during the closing stages of the Boreal period.

Recently (Blackburn, 1940; figure in Godwin, 1943), a peat from the Isle of Soay was described which agreed with this basal dating. Other Hebridean profiles examined begin as early as, or earlier than, this and reveal that the general trends of the curves are comparable with those from more southern stations (Blackburn, 1946 and mss.).

South Uist peats

(*a*) *Calvay.* This peat formed a cliff about 2 m. high on the east shore of the island and was completely exposed only at low tide. The lower 35 cm. consisted of a dark, buttery peat containing birch twigs. Above this the consistency was more fibrous, and the uppermost layers revealed a fibrous, grassy peat but little decomposed. Three layers like this characterize a number of relatively deep peats seen on the Outer Isles. A consideration of the pollen curves for this profile (Fig. 2) makes it clear that the base of this diagram displays a hazel maximum reading as high as 133 % of the total tree pollen. Alder, not represented at the base, remains low throughout the brushwood peat, and then rises steeply. Pine is but little in evidence in this locality, and it is birch which gives way to alder rather than pine. For this reason it seems desirable to concentrate on the change in type of the deposit, and the rapid rise of alder to a high value, in deciding at what level to indicate the end of the Boreal and the onset of the Atlantic period (the VI–VII zone transition of Godwin, 1940). In this case, the top of the brushwood peat, at a depth of 155 cm., reveals the birch and alder values as coincident. The close of the combined Atlantic and Sub-Boreal periods (Godwin's zone VII) is marked once again by qualitative difference in the peat, but this is less striking than the sudden fall in percentage of the total non-tree pollen (N.T.P.), significant of an increase in the forest cover of the island. Associated with this recovery is another hazel maximum. Subsequently, a heavy rise in the quantity of heather pollen signalizes the onset of the less favourable Sub-Atlantic period (zone VIII).

Further division of the zones, or more minute consideration of the details in respect to the pollen of individual species of tree, is not relevant to the subject in hand; nevertheless, the low values of elm, oak and lime, as well as the total absence of beech and hornbeam, should be noted as characterizing the diagram as a whole. However, an aspect of the graph which is of present significance is the incidence of the most frequent types of N.T.P. and of *Sphagnum* spores.

At this point it should be emphasized that such great quantities of these have had to be registered that it was found desirable to plot their values, calculated as percentages of total tree pollen, on a scale one-tenth of that used for the trees. A white line through the cross-hatching indicates 100 % on each of the curves. These high figures for N.T.P. would seem to suggest that the forest cover on the island, at least since the Boreal period, has never been close, and also that, in the Sub-Atlantic, there were limited numbers of trees, just as there are to-day. Despite this it is remarkable that no great difficulty has been encountered in scoring 150 tree-pollen grains at any level, although admittedly rather special methods of concentrating the pollen have been utilized. Obviously, in the Calvay area, heather predominated over grass in the sward, whilst sedges and cotton grass only manifested themselves sporadically in significant amounts. *Potentilla*, in all

probability *P. erecta*, present throughout in relatively small quantities, shows one high peak. *Sphagnum* attains significance in the bottom layers only.

(*b*) *Stoneybridge peat* (S.U.3). This peat likewise began to develop at a period of high hazel maximum, but the total depth of peat is only 75 cm. For this reason the graph has been plotted at twice the vertical scale of the Calvay series in order to facilitate comparisons. The bottom sample consisted of a brown mass of decomposed rock containing many distorted pollen grains. Above this followed 5 cm. of black, buttery peat with birch, succeeded by somewhat less humified peat containing cuticles of robust growths of *Phragmites* and some birch twigs, suggesting the existence of a loch somewhat higher than the present Loch Ollay. As in the Calvay peat, the upper layers were distinctly more fibrous.

Interpretation of this peat presents distinct difficulty although it might have been easier had it been more closely sampled. However, it was not suspected that the samples might be 500 years apart in point of time.

It is obvious that again the top of the black buttery material synchronizes with the rapid rise of alder. Hence, if we use the same criteria as before, this level represents the end of the Boreal period. Thus, in this area of South Uist, remains of Boreal peat are very scanty.

As the alder rises the birch falls, but the actual percentages remain well above those of the alder until well into the Atlantic. In all probability this is correlated directly with the occurrence of birch twigs indicating that the trees had grown on the site; in the neighbouring station (S.U.2), carrying no twigs, a typical rapid rise of alder to high values was manifested.

The end of zone VII can be determined by direct comparison with the Calvay diagram, though its features are not so striking.

On the whole the N.T.P. curves are steadier and more consistent than those of Calvay. Except for heather, with a small peak agreeing with the Boreal hazel maximum, all four curves begin at a low level, and rise to peaks in the upper Atlantic, falling in the Sub-Boreal and rising again in modern times. Grasses attain higher values, and heather is less frequent than on Calvay; this seems quite local and does not apply to S.U.2. The markedly higher values for *Potentilla* are conspicuous. *Sphagnum* alone differs completely, as it tends to maintain a moderate value throughout, with two small peaks.

In general it may be concluded that the likenesses between the two peat profiles illustrated are much more striking than their discrepancies. Other peats from both the Inner and Outer Isles show conspicuous differences in the relative amounts of the tree pollens, and in the type and quantity of N.T.P.'s and spores.

Peat from the Trapa *nut*

As has been stated, the minute supply of peat scraped from the surface hollows of the nut yielded a count of 140 tree-pollen grains. The percentages for the various species recorded on the two peat profiles just discussed were as follows: birch 44%, pine 7%, elm 3%, oak 14%, lime 0%, alder 33%, hazel 41%, willow 0%, ericoid 150%, *Sphagnum* 62%, grasses 53%, *Carex* 72%, and *Potentilla* 6%. In addition, odd pollen grains of plantain, dandelion, sundew and bur-reed occurred, as well as spores of ferns

and *Selaginella*, all of which had been detected at some level in one or both of the peats described. The lines drawn to indicate the above percentages are to be found between the two pollen diagrams, and will aid comparisons with them.

It will be apparent at once that the nut was not one that had floated from afar, but one which had originated in, and been washed out of, some nearby peat. It may have been derived from the Calvay exposure and subsequently carried upstream by the high tides which rush with tremendous force from Loch Eynort into Loch Ceann a' Bhaigh. Alternatively, it may have come downstream from Loch Iarras, or from some of the lochs and lochans in the Loch Ollay system between Stoneybridge and Bayhead. In the latter case it could not have been derived from the exact exposure sampled, as that was from a moorland peat cutting. Taking all the facts set out above into cognizance, the problem set is to select a 'time' position for the nut on the basis of the pollens observed.

For the general proportions of the forest trees, we might consider the post-Boreal sections of either diagram. A further limitation, fixed by the relatively low amounts of N.T.P. on the nut, leads our investigation to the earlier and closing parts of zone VII, since they alone have little N.T.P. The Sub-Boreal, however, shows a hazel maximum which precludes further consideration of that level. Thus there remain only parts of the two diagrams between the end of the Boreal and the rise of the N.T.P. to aid us in selecting the better match.

In the Calvay diagram the only part of this period which provides the correct relationship between birch and alder is just above the actual junction between zones VI and VII. Here the oak sinks too low, and hazel mounts too high whilst *Sphagnum* is practically absent; thus the 'fit' is only fair. On the other hand, the Stoneybridge peat has the right proportions of birch and alder at a depth of 50 cm., which is just below the middle of zone VII. Further investigation reveals an extraordinarily close match in the percentages of the other curves. Judging from these observations it can be safely said that examination of the pollen on the *Trapa* nut supports the hypothesis that it was derived from a peat on the shores of one of the ramifications of Loch Ollay. Further, these studies lead to the conclusion that the period at which it grew and was buried was some time in the first half of the Atlantic period.

Summary

1. A nut of *Trapa natans* was found in the wash cast up on the shores of the brackish Loch Ceann a' Bhaigh, on the Isle of South Uist, Outer Hebrides.

2. Peat from the nut yielded a satisfactory pollen count.

3. Two sample profiles of blanket peat from stations, respectively 1 mile south-east and 2 miles north-east, have been studied, and found to extend from the Boreal hazel maximum to recent times.

4. Comparison of the pollen counts from the *Trapa* nut shows a very close agreement with the general trend of both of these diagrams, but an almost perfect match was found in a level attributed to the middle of zone VII in the profile from the north-west, suggesting that in the Atlantic period *Trapa* grew in the lowlands to the west of the island which, to this day, are covered by a network of lochs and lochans.

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THE EMBRYOLOGY OF *ZEUXINE SULCATA* LINDL.

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(With 14 figures in the text)

Zeuxine sulcata, belonging to the tribe Neottinae (Orchidaceae) of Pfitzer (1889), is a plant of considerable interest. It belongs to that class of 'holosaprophytes' (Burgeff, 1931) which exhibits an extreme case of chlorophyll-lessness associated with other characters like the absence of a root system and a poor development of the vascular tissue. Perennation occurs by means of underground shoot buds (Joshi, 1933). The pollen and ovules are to a large extent sterile; the mode of reproduction is typically apomictic; nucellar embryony is frequent; and last, but not least, the megaspore tetrad itself is alleged to divide and produce a haploid embryo in many cases (Seshagiriah, 1941).

The life history was first studied by Seshagiriah, who (1932*a*) published a note entitled 'Development of the female gametophyte and embryo in *Spiranthes australis* Lindley', but later (1932*b*) rectified the name as *Zeuxine sulcata* Lindl. In 1934 he recorded a complete sterility of the pollen in this plant, followed by a fuller paper in 1941 describing the development of the embryo.

Since some of Seshagiriah's statements, particularly that concerning the origin of haploid embryos, appeared doubtful, I undertook a reinvestigation of the plant, and the results are set forth in this paper.

The material was collected from plants growing around Bangalore. The habitat and ecological associations are very characteristic: the plant thrives in open marshy regions in association with *Drosera burmanni*, species of *Eriocaulon* and certain grasses and sedges. For the last five years I kept under observation several patches of this plant and found that the flowering season commences in December or January and ends in early March. This is in agreement with the observations of Cook (1908), but Seshagiriah (1941), also working at Bangalore, writes that the flowering period extends from September to October. This I am unable to confirm from my experience of the plant.

Microsporogenesis and male gametophyte

Sections of young anthers show that the parietal tissue consists of the epidermis, followed by a layer of cells which probably represents the endothecium, one, or occasionally two, middle layers, and last of all a single layer of uninucleate tapetum. The pre-meiotic stages in the pollen mother cells proceed normally, but I found irregularities setting in soon after the pairing of the chromosomes. During the first division several laggards were noticed, and the inequality in the number of chromosomes at the two poles was quite evident at the telophase stage. The second division is often completely suppressed, but it is not always so and the formation of microspore tetrads is by no means so rare as supposed by Seshagiriah. The divisions are of the simultaneous type as in other orchids, and the microspores of a tetrad do not separate from one another. The first division of the microspore nucleus is also very irregular, and the maximum amount of

degeneration of the pollen seems to occur at this stage. In spite of these irregularities and accompanying degenerations, I found a small percentage of perfectly normal two-celled pollen grains, some of which germinated in sugar solution and put out short pollen tubes showing the tube and generative nuclei.

Ovule and embryo sac

I do not propose to deal here with the structure of the ovary and ovule, as this will form the subject-matter of a separate paper which is in course of preparation. The hypodermal archesporial cell is mounted on an axial row of three to four nucellar cells as in many other orchids. This functions directly as the megaspore mother cell, and up to the onset of the first metaphase of the reduction division my observations are in agreement with those of Seshagiriah. After this stage he and I differ in important respects, and therefore I shall describe my observations in some detail.

During the first metaphase, the distribution of the chromosomes on the spindle is highly abnormal and variable. Several chromosomes were seen to lag behind, and in the majority of instances degeneration sets in soon after the stage represented in Fig. 1, i.e. before the completion of the anaphase. Occasionally when the division did proceed up to the anaphase stage, some of the chromosomes did not pass to either pole but lagged behind at the equatorial region (Fig. 2); the spindle substance then faded away and all the chromosomes became clumped into a darkly staining mass, indicating a cessation of development.

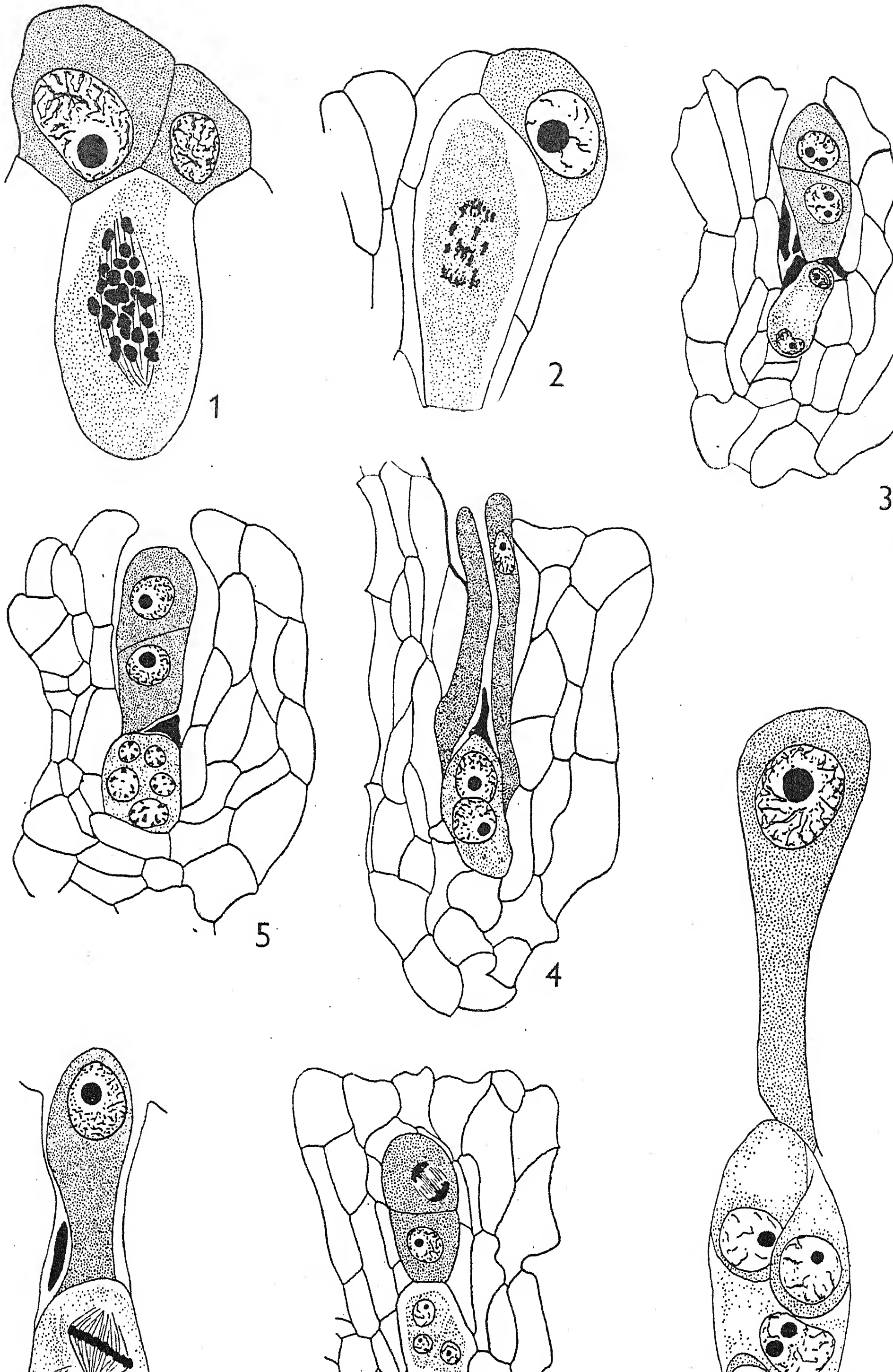
Only in rare instances is the first division completed. Even in such cases no wall is laid down (as should be the case) between the daughter nuclei (Fig. 4); in one instance a distinct vacuole was seen however (Fig. 3), and in a couple of ovules the embryo sac showed 4–6 nuclei of different sizes without any definite organization or polarity (Fig. 5). In another case (Fig. 6) the embryo sac showed two division figures, and still another (Fig. 7) had four nuclei which seemed to be surrounded by individual masses of cytoplasm. Only one instance (Fig. 8) was seen where the embryo sac was more or less normally organized, with an egg cell, a synergid, the secondary nucleus and a single unusually elongated antipodal cell. Apart from these few cases, the development did not seem to proceed beyond the first division of the megaspore mother cell, a condition which is obviously due to the meiotic irregularities noted already.

Embryo

The most extraordinary feature of Seshagiriah's paper is the alleged origin of the embryo directly from the linear tetrad of megaspores, derived as a result of the meiotic divisions in the megaspore mother cell. Especial attention was paid by me to this aspect of the life history.

Legend to Figs. 1—8.

Fig. 1. Megaspore mother cell in anaphase; the two enlarged cells above it belong to the nucellar epidermis. ×1480. Fig. 2. Same, more advanced stage, showing the commencement of degeneration and arrest of further development. ×1480. Fig. 3. Two-nucleate embryo sac and two-celled nucellar embryo. ×740. Fig. 4. Two-nucleate embryo sac with two greatly elongated nucellar cells. ×740. Fig. 5. Abnormal five-nucleate embryo sac and a two-celled nucellar embryo. ×740. Fig. 6. Abnormal embryo sac with two metaphase spindles and an elongated nucellar cell on top. ×1480. Fig. 7. Abnormal embryo sac with four nuclei, each surrounded by some cytoplasm. Note nucellar embryo on top. ×740. Fig. 8. Embryo sac showing egg cell, one synergid, the secondary nucleus and a single antipodal cell. Note greatly elongated nucellar cell above. ×1480.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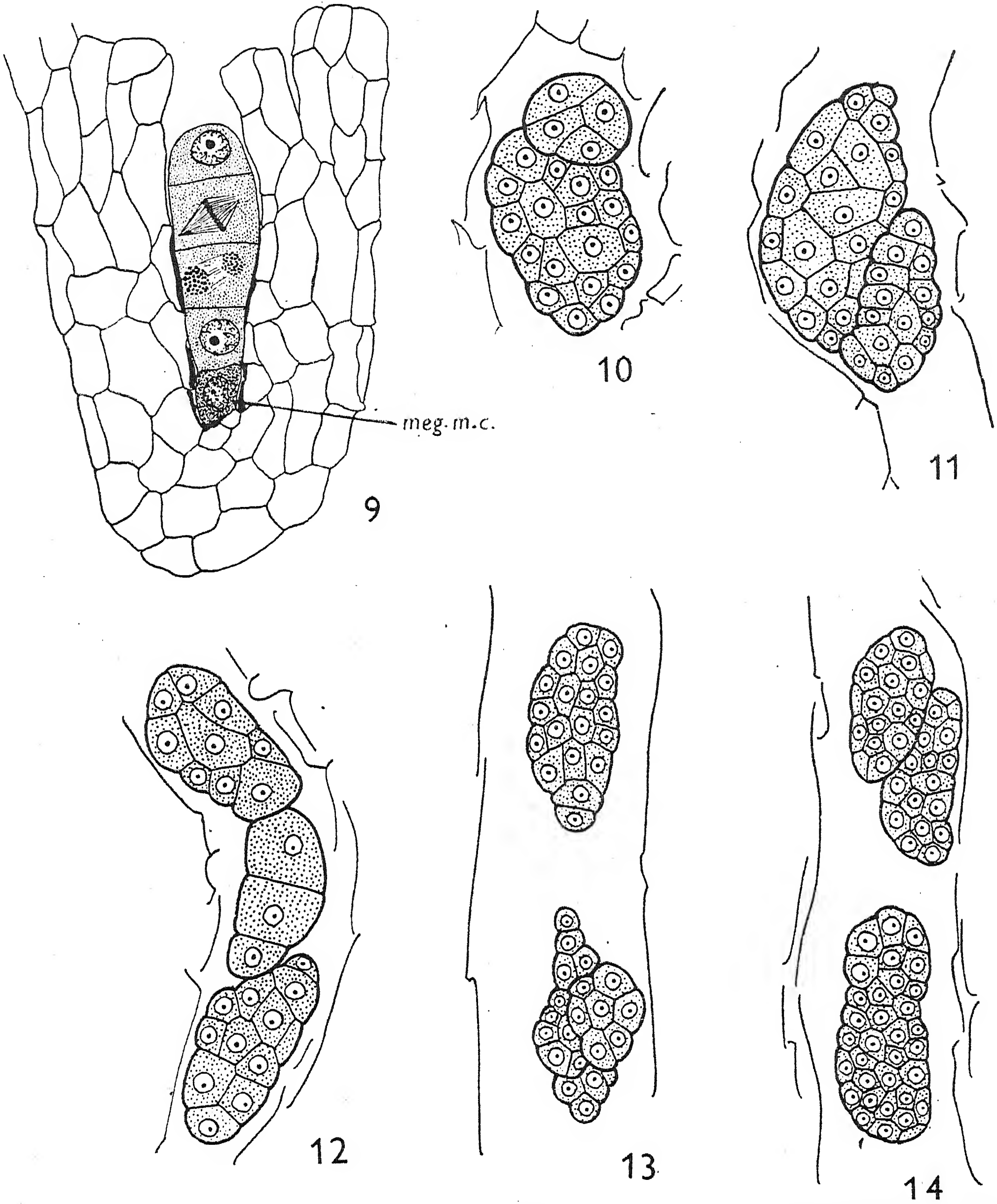

Fig. 9. A four-celled nucellar embryo with the two central cells in division. Note the degenerating megaspore mother cell (*meg.m.c.*) at the base of the embryo. × 1200. Figs. 10–14. Stages in the formation of plural embryos. × 84.

Seshagiriah's figs. 1–14, which illustrate the development of the haploid embryo, at first appear so convincing that a second thought is scarcely necessary. But in spite of a careful study I could find no evidence of normal megaspore formation, to say nothing of the megaspores acting jointly to produce an embryo. On the other hand, the cells of the nucellar epidermis show a remarkable capacity for enlargement and division, leading to the formation of adventive embryos. In my Figs. 6 and 8 one cell of the nucellar epidermis has elongated and is ready to divide. In Fig. 4 there are two such cells. In

Figs. 3 and 5 a transverse division has taken place leading to the production of two-celled embryos, and in Fig. 7 there is a further division of the upper of the two cells. Some additional divisions lead to the stage shown in Fig. 9, which is of special interest as it is very similar to Seshagiriah's fig. 12, interpreted by him as a haploid embryo derived from the megaspore tetrad. That this interpretation is untenable will now be easily understood by a reference to the previous stages (Figs. 6, 8, 5 and 7). What we see here in Fig. 9 (also Seshagiriah's fig. 12) is a nucellar embryo, formed by the divisions of a cell of the nucellar epidermis, with the degenerating megaspore mother cell still recognizable at the bottom in my figure (*meg.m.c.*). In addition, a counting of the chromosomes in the third cell of the embryo (proceeding from the micropylar end downward), which is in late anaphase, definitely showed considerably more than 22 chromosomes, which is the reported haploid chromosome number in the plant (Seshagiriah, 1941).

Seshagiriah does not mention the number or percentage of such embryos, but considering the prominence given by him to this phenomenon one is likely to think that this must be occurring in at least 50% of the ovules. I counted the chromosomes in about ninety young and actively growing embryos, and in all of them the number ranged between 44 and 48, which is very near the diploid number ($n = 22$).

Sometimes two to three embryos are seen in a single ovule. These may arise, either because more than one nucellar cell begins to divide or sometimes by a cleavage or proliferation of the original embryo (see Figs. 10–14) as has already been found in some other orchids (Swamy, 1942, 1943).

Summary

In *Zeuxine sulcata* most of the pollen is sterile. In the ovule degeneration starts at the megaspore mother cell stage, and few, if any, functional embryo sacs are formed, which, however, become arrested at various stages of development. Embryos arise apomictically from the cells of the nucellar epidermis and contain the diploid number of chromosomes. Polyembryony may be due either to the independent growth and development of more than one cell of the nucellar epidermis or by further proliferation, budding or cleavage of a single embryo. There is no evidence whatever of the occurrence of haploid embryos supposed to arise directly from the linear row of megaspores.

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A CYTOLOGICAL AND ECOLOGICAL STUDY OF SOME BRITISH SPECIES OF *GLYCERIA*

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(With 1 figure in the text)

Owing to the presence of certain discrepancies in the published work on some species of *Glyceria*, it was decided, in September 1943, to make a cytological and ecological study of the following forms:

(1) *Glyceria declinata* Bréb.
(2) *Glyceria fluitans* (L.) R.Br.
(3) *Glyceria plicata* Fries.
(4) *Glyceria fluitans* × *Glyceria plicata*, a possible hybrid.
(5) *Glyceria maxima* (Hartm.) Holmb.

Table 1. *The somatic chromosome numbers of some of the species of* Glyceria

Species	2*n*	Author
G. declinata Bréb.	20	Maude (1940)
G. plicata Fries	28	Stählin (1929)*
	40	Maude (1940)
G. fluitans (L.) R.Br.	28	Stählin (1929)*
	40	Maude (1940)
	20, 40	Church (1942)
G. maxima (Hartm.) Holmb. (*G. aquatica* var. *typica* Aschers.)	56	Avdulov (1928)*
G. maxima (Hartm.) Holmb. (*G. aquatica* (L.) Wahl.)	56	Stählin (1929)*
G. maxima (Hartm.) Holmb.	60	Church (1944, unpublished)
G. arundinacea (M.B.) Kunth. (*G. aquatica* var. *arundinacea* Aschers.)	28	Stählin (1929)*
G. nervata (Willd.) Trin. (*G. striata* (Lam.) Hitchc.)	28	Stählin (1929)*
G. striata (Lam.) Hitchc.	20	Church (1942)
G. grandis S. Wats.	28	Nielson (1939)*
	20	Church (1942)
G. elata (Nash) Hitchc.	20	Church (1942)
G. canadensis (Michx.) Hitchc.	40	Church (1942)
G. melicaria (Michx.) F. T. Hubb.	40	Church (1942)
G. borealis (Nash) Batch.	20	Church (1942)
G. septentrionalis Hitchc.	40	Church (1942)
G. occidentalis (Piper) J. C. Nels.	40	Church (1942)
G. leptostachya Buckl.	40	Church (1942)
G. pallida (Torr.) Trin.	14	Church (1942)
	20	Matsuura & Sûto (1935)*
G. neoglea Steud.	14	Church (1942)
G. pauciflora Presl.	14	Church (1942)
G. erecta Hitchc.	14	Church (1942)

The specimens were collected in the late summer of 1943 from various localities in the Oxford district. In addition, specimens of *G. declinata*, *G. fluitans* and *G. plicata* were obtained from Kew Gardens and were of the same material as that studied by Maude (1939). Herbarium specimens have been kept for reference.

The results of chromosome counts by other workers on this genus are given in Table 1. Whatever the causes of the discrepancies shown therein, an examination of the British representatives of these species seemed justified.

* See Maude (1939) and references there quoted.

Cytological technique

(1) *Method of growing the plants*

Somatic chromosome counts were made from actively growing root tips. In many cases these roots could be taken immediately from the carefully washed underground parts of the plants. All specimens, however, were grown in tap water which was renewed once or twice daily. Care was taken to see that no dead or decaying organic material was present in the water, as under such conditions the roots soon became slimy and useless for cytological study. The plants were afterwards removed to soil in pots. It may be noted that after about 7 days in water, *Glyceria* plants became chlorotic and unhealthy in appearance, but soon recovered on return to the soil.

(2) *Choice of fixative*

The type of fixative used greatly influences the ultimate staining results, and for any particular species the best must be found by empirical methods. The final choice will, of course, depend on the requirements of the worker. The first essentials for counting the somatic complement are that the chromosomes should be well stained and spaced with little or no overlapping.

It may also be desirable to obtain an accurate representation of the morphology of the chromosomes, especially the constrictions, which may be of value taxonomically. Flovik, in his study of arctic grasses (1938), found that for this latter purpose, the osmic fixatives such as La Cour's 2BD, 2BE were more satisfactory than the formalin-chrom-acetic types. On the other hand, the use of these latter types resulted in the chromosomes being well spaced on the metaphase plate and therefore more readily countable.

In this study, Müntzing's modified Navashin fixative was tried first with very satisfactory results. Belling's Navashin gave similar results. 2BD and 2BE were also tried. The chromosomes, however, remained less well stained although their morphology could be more readily determined. Owing to the fact that the chromosomes were small and their number high, the ultimate choice of fixative was governed by the ease with which the somatic number could be counted. The majority of the *Glyceria* preparations were, therefore, fixed in Müntzing's modified Navashin solution (1933).

La Cour's alcohol-chloroform method (Darlington & La Cour 1942) followed by Hancock's schedule (1942) were used with good results. Sections of 14μ thickness were cut. The chromosome counts were made with a Zeiss binocular microscope using a Zeiss apochromatic 1·5 mm. objective and compensating $15\times$ eyepieces.

Results of the somatic chromosome counts

The results of the somatic chromosome counts done on the root-tip cells of the five British forms of *Glyceria* examined in this study are summarized in Table 2.

The $2n$ values given below represent the most frequently occurring values obtained. The somatic number of the possible hybrid is in all probability 40. This supports the view that these specimens are indeed of hybrid origin and that the parents are the tetraploids, *G. fluitans* and *G. plicata*. Great difficulty was experienced in counting the chromosomes of *G. maxima*, but it seems that the somatic number may be 60.

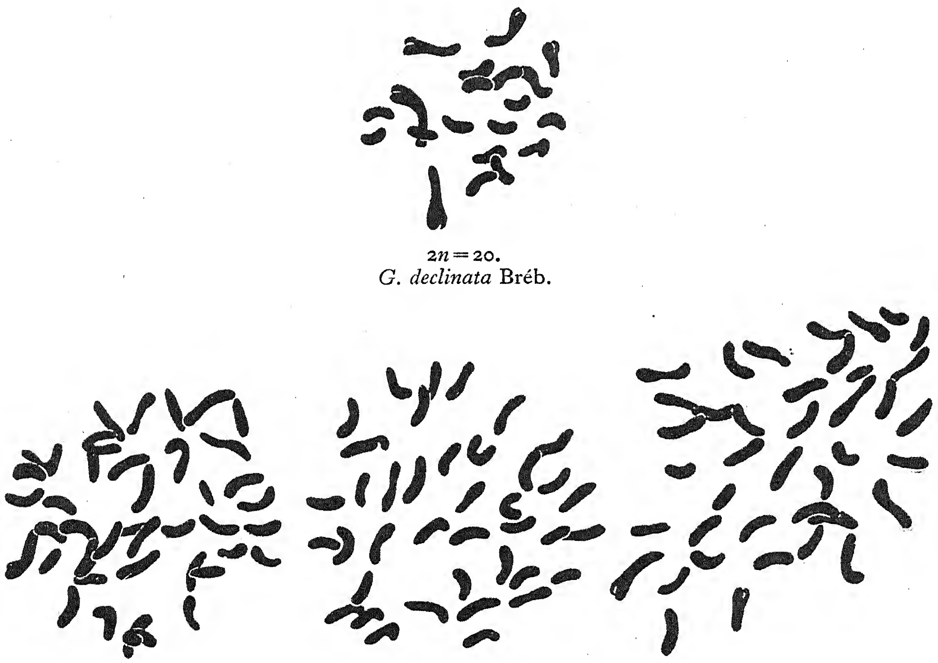
Unfortunately, time did not permit examinations of the meiotic chromosomes of the pollen grains.

The chromosomes themselves are small, varying in length from about 1·2 to 2·5 μ in the four smaller forms of *Glyceria*. Those of *G. maxima* were found to be larger.

Thus *G. declinata* is a diploid; *G. plicata*, *G. fluitans* and their hybrid are tetraploids; and *G. maxima* is a possible hexaploid. The basic number of these British representatives of the genus seems, therefore, to be 10 (or 5).

Table 2. *The somatic chromosome counts of* Glyceria

Species	No. of plants examined	No. of plates examined	$2n$	Length of chromosome in μ
G. declinata	6	19	20	1·2–2·5
G. plicata	7	26	40	1·2–2·5
G. fluitans	4	11	40	1·2–2·5
G. plicata × *G. fluitans*	6	24	40	1·2–2·5
G. maxima	2	5	60?	(2·9–4·1)
Total	25	85		



$2n = 20$.
G. declinata Bréb.

$2n = 40$.
G. plicata Fries

$2n = 40$.
G. plicata × *G. fluitans*.

$2n = 40$.
G. fluitans (L.) R.Br.

Fig. 1. The somatic chromosome complements of 5 British *Glycerias*. × 4267.

Correlation between size of cell and chromosome number

In plants, the chromosome number can often be correlated with the size of the cells, in particular, the size of the guard cells of the stomata and of the pollen grains. Measurements of these two types of cells in the *Glycerias* were taken to see whether any such correlation existed in this genus.

(1) *Guard cells and chromosome number*

A preliminary examination of the stomata of the five forms of *Glyceria* was carried out to get an idea of the range in size of the guard cells and their distribution. Measurements were then taken from as many leaves as possible, which were chosen carefully in order to ensure that all samples were approximately of the same age. The second and third youngest leaves were found to be sufficiently mature and uniform for this purpose. The plants used had been growing under identical conditions for 4 months.

Portions of the epidermis were taken from the underside of the leaf, midway between the 'midrib' and margin, and about halfway along the length of the leaf. These strips were then transferred quickly to a drop of spirit on a clean slide and covered with a cover-slip. The length of the guard cells was then measured by means of a micrometer in one of the 15 × eyepieces. A × 60 objective was used. The results obtained are shown in Table 3.

Table 3. *Average lengths of guard cells of* Glyceria

Species	No. of plants examined	No. of leaves examined	No. of measurements	Mean length in μ, and S.E. of mean
G. declinata	5	10	100	34.6 ± 0.28
G. plicata	4	9	100	37.5 ± 0.29
G. fluitans	4	8	100	37.5 ± 0.32
G. plicata × *G. fluitans*	4	8	100	38.1 ± 0.35
G. maxima	2	5	100	45.2 ± 0.29
Total	19	40	500	

Table 4. *Pollen-grain diameters of* Glyceria

Species	No. of grains examined	Mean diameter of grain in μ, and S.E. of mean
G. declinata	20	38.9 ± 0.28
G. plicata	20	47.0 ± 0.69
G. fluitans	20	45.1 ± 0.49
G. plicata × *G. fluitans*	20	(34·4, all empty)
Total	80	

From this table it can be seen that *G. declinata*, the diploid, is significantly different from each of the three tetraploids. Moreover, the three tetraploids, *G. plicata*, *G. fluitans* and their hybrid, do not differ significantly among themselves. *G. maxima*, on the other hand, is extremely different from either the diploid or the tetraploid forms.

(2) *Pollen-grain diameter and chromosome number*

Samples of pollen grains were taken from ten mature anthers from one plant of each of the four smaller *Glycerias*. Pollen of *G. maxima* was not measured.

The grains were shaken on to a slide with a mixture of 1 part glycerine and 1 part acetocarmine and covered by a cover-slip. Twenty of the largest and fullest grains were measured for each of these *Glycerias*. A 15 × eyepiece and × 60 objective were used. The results obtained are shown in Table 4.

Although the number of measurements is rather small, there is a significant difference

between the mature pollen-grain diameter of the diploid and the tetraploid species. The exact cause of the formation of the small, empty grains of the hybrid is not known. No studies of the development of the pollen grains were made.

Ecological notes on the *Glycerias*

From the very preliminary work so far carried out, it appears that the diploid, *G. declinata*, seems to be the most drought-tolerant of the group. It was found in dried-up ponds which were shallow and often mere depressions at a considerable distance from streams and permanent ponds (e.g. G 1, G 1 A, G 18). One specimen (G 19) was found in the dried ruts of a cart track on Otmoor. In contrast to this, *G. fluitans*, a tetraploid, was found in wetter habitats, such as ditches and stream edges, where there was often standing water throughout the year. *G. plicata* and the hybrid, also tetraploids, appeared to occupy habitats intermediate in wetness. The hybrid was often found in the vicinity of one or other of the parents.

Although more study is required before any definite statements can be made concerning the ecology of these plants, it does seem that these species, morphologically and cytologically distinct, have also some ecological differences.

In recent years it has been found that the polyploid members of a species or genus often occupy habitats with more extreme environmental conditions than the diploid

Table 5. *The results of various workers of the somatic chromosome counts of these five forms of* Glyceria

Species	Stählin (1929)*	Church (1942)	Maude (1939–40)	FitzPatrick
G. declinata Bréb.	—	—	20	20
G. plicata Fries	28	—	40	40
G. fluitans R.Br.	28	20, 40	40	40
G. plicata × *G. fluitans*	—	—	—	40
G. maxima (Hartm.) Holmb.	56	60	—	60?
	Avdulov (1928, unpubl.)			
G. maxima (Hartm.) Holmb.	56	—	—	—
Basic number	7	10	10	10

members, thereby extending the range of the group as a whole. In *Glyceria* the diploid species is *G. declinata*, and inhabits dryer habitats than the tetraploid forms. Whether the genus *Glyceria* supports this theory concerning polyploids or not, will depend on which of the two habitats—the dryer or the wetter—one considers as being the more specialized.

Discussion

(1) *Comparison of the results with those of other workers*

In order to compare the results of this study with those of other workers, the chromosome numbers have been listed in Table 5. It will be noticed from this table that the results obtained for *G. declinata*, *G. plicata* and *G. fluitans* agree with those of Maude (1939). Church (1942) obtained the somatic number 40, for *G. fluitans* in his work on the American members of the genus. He also found a diploid type of *G. fluitans* which has so far not been found in this country. Stählin (1929)*, on the other hand, obtained the somatic number 28 for both *G. plicata* and *G. fluitans*.

* Quoted from Maude (1939).

Maude's results of 1939–40, supported by those obtained here and by Church, would therefore seem to be correct, at least for British and American representatives of the genus. It is difficult to find an explanation for the low somatic numbers given by Stählin. It is inconceivable that a mistake could have been made in the counting of the chromosomes, particularly as the difference between the two sets of results is as much as 12. It may be stated here that in the present study the name of each plant was checked by a competent taxonomist, in order to minimize possible errors in identification.

No previous cytological work seems to have been done on the hybrid, *G. plicata* × *G. fluitans*. The results for these specimens are what one might have expected.

As for *G. maxima*, the results obtained in this study differ from those of Continental workers. Church (1944 unpubl.), however, obtained the number 60 for American material of the species. It seems reasonable, therefore, to suppose that the somatic number of *G. maxima* may be 60, though it is possible that other cytological forms might be found if a more extensive examination of this species were made.

(2) *The basic number of the genus* Glyceria

The basic number of this genus was previously given as 7 (Maude, 1939). This number, presumably, was obtained from the results of Stählin (1929)* and Avdulov (1928)*, whose somatic numbers for various species of the genus are multiples of 7.

As a result of her work on some British members of the genus, Maude suggested that 10 may be its basic number. This is supported by the results of this study, those of Church (1942, and unpublished), and by Matsuura & Sûto (1935)*. There is no doubt that 10 (or 5) is the most frequent basic number of these species so far examined.

It is interesting to note, however, that the somatic number obtained for *G. pallida* by Matsuura & Sûto is 20, whilst that by Church is 14. A similar discrepancy occurs in the results for *G. grandis* where Church finds 20 somatic chromosomes, and Neilson 28, and for *G. striata* where Church finds 20 chromosomes and Stählin 28.

Explanations for such discrepancies are difficult to find. It would seem that great care is necessary in cytological work of this kind, in case the somatic numbers already published influence the interpretation of the metaphase plates of species which are yet to be studied.

The four American species studied by Church with 14 chromosomes are stated by him to differ from the others he examined both morphologically and by the possession of larger chromosomes. It is possible that these differences may merit a revision of their taxonomic treatment. On the other hand, it may be that both 10 and 7 exist as basic numbers in the genus *Glyceria*.

Thus, although 10 (or 5) would seem to be the basic number for British and most American representatives of the genus *Glyceria*, further work is necessary before it can be stated that specimens with somatic numbers which are multiples of 7 also occur.

Summary

A cytological and ecological study of some British representatives of the genus *Glyceria* was undertaken in the autumn of 1943. The species examined were *G. declinata* Bréb., *G. plicata* Fries, *G. fluitans* R.Br., a possible hybrid *G. plicata* × *G. fluitans*, and *G. maxima* (Hartm.) Holmb. Chromosome counts were made from root tips, fixed in Müntzing's modified

* Quoted from Maude (1939).

Navashin solution and stained according to Hancock's schedule (1942). *G. declinata* was found to be a diploid with 20 chromosomes, *G. plicata*, *G. fluitans* and their hybrid, tetraploids with 40 chromosomes, and *G. maxima*, a possible hexaploid with 60 chromosomes. The basic number of the British members of the genus seemed to be 10 (or 5). Positive correlations between chromosome numbers on the one hand and stomatal length and pollen-grain diameter on the other were found. Besides being morphologically and cytologically distinct, these species also had some ecological differences. *G. declinata* seemed to be the most drought-tolerant of the forms examined. The cytological results of other workers were discussed and compared with those obtained in this study. It would appear that Maude's results and those obtained here are the numbers which must be accepted for British representatives of the genus.

I am greatly indebted to Mr C. E. Hubbard of the Royal Botanic Gardens, Kew, for kindly collecting most of my specimens, identifying the material used in this study and for discussing taxonomic problems with me. I also wish to express my grateful thanks to Prof. A. R. Clapham for his constant encouragement and assistance, and to other friends who have helped me.

APPENDIX

List of plants

Serial no.	Date	Place	Habitat
		I. *Glyceria declinata* Bréb.	
G1	18. viii. 43	River Cherwell, Oxford	Bottom of dried-up pond
G1A	18. viii. 43	,,	,,
G18	19. viii. 43	,,	,,
G19	23. viii. 43	Nr. Otmoor and Beckly	Green lane, in mud of cart track
G22	24. viii. 43	Bletchington, nr. Diamond Farm	Dried pond
K2	3. ix. 43	Kew Gardens	Pond
		II. *G. plicata* Fries	
G2	18. viii. 43	Kennington	Edge of pool
G4	18. viii. 43	,,	Edge of pool on drying bank
G16	19. viii. 43	Pixy Mead, Oxford	Damp depression
G17	19. viii. 43	,,	Another damp depression
G20	23. viii. 43	Bayswater Brook	In stream by roadside
G21	24. viii. 43	Bletchington, nr. Diamond Farm	Dried pond
K3	3. ix. 43	Kew Gardens	Pond
		III. *G. fluitans* R.Br.	
G6	18. viii. 43	Kennington	Damp depression in a meadow
G11	19. viii. 43	Wolvercote	Damp mud near railway line
G15	19. viii. 43	Pixy Mead, Oxford	Damp depression
K1	3. ix. 43	Kew Gardens	Pond
		IV. *G. plicata* × *G. fluitans*	
G8	18. viii. 43	Kennington	Shallow ditch
G9	18. viii. 43	River Cherwell, nr. Marston	Pond margin with *G. plicata*
G10	18. viii. 43	Kennington	Shallow ditch with *G. maxima*
G12	19. viii. 43	Wolvercote	Damp mud by wall
G13	19. viii. 43	,,	Drying bank of ditch
G14A	19. viii. 43	,,	Damp mud by railway
		V. *G. maxima* (Hartm.) Holmb.	
M1	12. x. 43	River Cherwell, Oxford	Edge of river
M2	14. x. 43	River Isis, Oxford	,,

G19, G22, G20 were collected by Dr A. R. Clapham.
G18, G16, G17, G11, G15, G13, G14A, G12 by Mr C. E. Hubbard, Dr A. R. Clapham, and Mrs J. M. FitzPatrick.
M1 and M2 were collected by Mrs J. M. FitzPatrick.
All the others were collected by Mr C. E. Hubbard.

The main diagnostic features of the three smaller British species of Glyceria

	G. fluitans R.Br.	*G. plicata* Fries	*G. declinata* Bréb.
Leaf blade	Bright green, acute, sometimes floating, 5–25 cm. long	Dark green, acute, 5–30 cm. long	Greyish green, short, often stiff, 3–18 cm. long
Sheath	Smooth	Rough and sulcate	Smooth
Panicle	Sparingly branched in lower parts or simple throughout, lower branches usually in pairs. Panicle contracted in fruit, the branches appressed to rachis	Much branched, typically relatively broad spreading in fruit, lower branches up to 5	Simple, sparingly branched at least above, often curving upwards, lower branches single or paired, rarely ternate
Florets	Many (8–16) acute florets per spikelet, 18–35 mm. long	Many (7–16) obtuse florets per spikelet, 10–25 mm. long	Fewer (9–15) obtuse florets per spikelet, 13–25 mm. long
Lemmas	Lanceolate-oblong, acute or obtuse, 6–7·5 mm. long	Broadly elliptic-oblong, 4–5 mm. long	Elliptic-oblong, shallowly 3-lobed or 3-toothed at apex, 4–5 mm. long
Palea	Acuminate, shorter or just surpasses lemma	Very obtuse, shorter or just equal to lemma	Acuminate, longer than lemma
Anthers	5 × long as broad, 2–3 mm. long	3 × long as broad, 1–1·5 mm. long	2 × long as broad, 0·8–1 mm. long
Caryopsis	Oblong elliptical, 2·5–3 mm. long	Elliptic-oblong, 2 mm. long	Oblong, 0·8–1 mm. long

Note on the hybrid G. plicata × G. fluitans

Although the six plants, G8, G9, G10, G12, G13, G14A, are almost certainly hybrids between *G. plicata* and *G. fluitans*, Mr C. E. Hubbard informs me that they differ somewhat from the authentic material of *G. pedicellata* Towns. This latter form has longer pedicels, more obtuse lemmas, shorter anthers, and more profusely branched panicles than the hybrid plants examined in this study. Our plants of the putative hybrid *G. plicata* × *G. fluitans* are on the whole nearer to *G. fluitans*, whereas *G. pedicellata* is nearer to *G. plicata*, although many of the characters of each hybrid are intermediate between the two parent species.

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VEGETATIVE MORPHOLOGY AS A GUIDE TO THE CLASSIFICATION OF THE PAPILIONATAE*

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(With 6 figures in the text)

An intensive study of the morphology of the vegetative shoot in Leguminosae has resulted in the recognition of the systematic value of a number of characters altogether foreign to the orthodox taxonomy of the family. The nature of these new characters has already been described (Dormer, 1945 *a*); it remains to discuss their impact on the classification of the family. At present only the Papilionatae can profitably be considered, as it has been impossible to obtain sufficient material of Mimosoideae or Caesalpinioideae.

For the present purpose we may regard the arrangement given by Taubert (1891) as the generally accepted standard classification of Papilionatae. Other published treatments differ rather in the arrangement of the tribes and subtribes than in their composition.

Probably a majority of systematists would now be prepared to admit that some of the tribes contain genera which are not really closely related to each other, but the criteria which have so far been employed have not proved adequate to the task of redistributing these genera.

The key to the problem appears to lie in a relatively trivial character. Throughout the Leguminosae, each leaflet is provided with a basal pulvinus which is responsible for most of the movements of the leaflet, but foliar pulvini, each of which moves an entire leaf, are not of such universal occurrence. A foliar pulvinus, situated at the base of the petiole, is constantly present in Mimosoideae and Caesalpinioideae, but is lacking in a considerable proportion of the Papilionatae. All species in which a leaf consisting of a single leaflet is provided with a basal pulvinus must perforce be left out of the present discussion, since it is impossible at present to decide whether such a pulvinus is to be regarded as foliar or foliolar. Omitting, for this reason, the Podalyrieae of the southern hemisphere, the Genisteae, and some isolated forms in other tribes, the remainder of the Papilionatae may be divided into a pulvinate and an epulvinate series, as shown in Table 1.

It may be shown that the particular arrangement of the Papilionatae given in this table, to which there are no known exceptions, has a number of remarkable properties.

An attempt has been made to indicate the geographical distribution of the various groups. O denotes a group having most of its genera and species in the Old World, N a predominantly American group. When these letters are doubled, it is to be understood either that the group in question is entirely confined to the specified hemisphere, or that there is some independent evidence to show that it originated there. In assessing the significance of the table, much greater weight must be given to the doubled letters. The five groups marked W are so generally distributed that it is impossible to say with any degree of probability that they belong to one hemisphere rather than the other. Liable

* This paper embodies the principal taxonomic results of an unpublished Ph.D. thesis accepted by the University of London.

though this procedure undoubtedly is to serious errors of judgement, several important facts seem to be established beyond question.

In the first place, it is clear that much less certainty as to place of origin has been expressed in the pulvinate column than in the epulvinate. This is due to the fact that pulvinate groups are, on the whole, much more widely distributed than epulvinate.

Secondly, the pulvinate groups are not only more numerous than the epulvinate, but they are also on the average much larger. The first three entries in the pulvinate column represent large tribes, any one of which contains almost as many genera as the whole of the epulvinate series put together.

It would seem to follow, by Willis's principle, that the pulvinate series is the older, and that the pulvinate condition is the primitive one. This interpretation is supported by the following considerations.

Table 1

	Pulvinate		Epulvinate
W	Sophoreae	OO	Trifolieae
N	Dalbergieae	OO	Loteae
W	Phaseoleae	W	Podalyrieae (northern genera)
W	*Abrus*	OO	Vicieae, except *Abrus*
	Subtribes of Galegeae		
W	*Glycyrrhiza*	OO	Astragalinae, except *Glycyrrhiza*
O	Tephrosiinae, except *Galega*	OO	*Galega*
NN	Robiniinae	OO	Coluteinae
N	Brongniartiinae		
NN	Psoraleinae		
O	Indigoferinae		
	Subtribes of Hedysareae		
O	Desmodiinae	OO	Coronillinae
N	Stylosanthinae	OO	Euhedysarinae
N	Aeschynomeninae		
NN	Patagoniinae		

There is a distinct correlation between the presence or absence of a foliar pulvinus and the general habit of the plant. Every tribe, subtribe, or genus mentioned in the epulvinate column of the table is predominantly herbaceous, whereas in the pulvinate series there are several groups which are predominantly or entirely woody. Furthermore, while the pulvinate series contains some dozens of genera of large forest trees, it is extremely rare for an epulvinate species to exceed the stature of a shrub.

Attention may next be drawn to the fact that of the epulvinate groups no less than five are characterized by uniformly dimerous phyllotaxy, and no epulvinate group is predominantly polymerous, while in the pulvinate series *Abrus* and *Glycyrrhiza* are entirely polymerous, Sophoreae and some other groups predominantly so, and only in the Phaseoleae is there any noteworthy proportion of dimerous species.

In the list of primitive and advanced characters already published (Dormer, 1945*a*, Table 1) the pulvinate condition has been treated as primitive on the evidence of these correlations.

The importance of the distinction between the pulvinate and epulvinate series is emphasized by the facts set out in Table 2. The differences between pulvinate and epulvinate species are very impressive when studied in living plants. It is difficult to escape the conclusion that the whole metabolism is different in the two groups—in particular the pulvinate forms are characterized by much more pronounced secretory

activity. Waksman (1927, p. 136) gives a table, based on cross-inoculation experiments, showing the various species of Leguminosae known to be infected by different strains of nodule bacteria. Some strains are known to be capable of infecting species belonging to a number of different tribes, so that it is interesting to note that no strain is known to infect both pulvinate and epulvinate species. It is also significant that, although exceptions can easily be pointed out, the basic chromosome number in pulvinate species is generally greater than 8, while in epulvinate species it is 8 or less.

It is not suggested that all the features characteristic of pulvinate types are therefore necessarily primitive. It is highly improbable, for example, that the ancestral Leguminosae had multilacunar nodes or anomalous secondary thickening, but they may have been endowed with a certain potentiality for developing these features, a potentiality which their epulvinate descendants have lost.

Table 2

Features common in the pulvinate types, rare or unknown in epulvinate:

- Stipels
- Ridge bundles in the petioles and rachises (Watari, 1934)
- Anomalous secondary thickening
- Secretory reservoirs
- Longitudinal walls in the epidermal hairs, making them multiseriate
- Subsidiary cells to the stomata of the leaves
- Multilacunar nodes (Sinnott, 1914; Watari, 1934)
- Opposite position of the first two leaves of the seedling

Features common in epulvinate types, extremely rare in pulvinate:

- Closed vascular systems

Returning for a moment to the geographical implications, it appears from Table 1 that all the groups which there is any adequate reason for regarding as of American origin are pulvinate, and that almost all the epulvinate forms can be assigned with reasonable probability to an Old World ancestry. It follows that the epulvinate condition must be supposed to have originated in the Old World. The occurrence of a few tribes having pulvini, yet presumably of Old World origin, in no way affects this view.

There follow some observations on the structure and affinities of some tribal and subtribal groups.

SOPHOREAE

Most of the species which have been examined exhibit in a typical form the type of vascular system which has elsewhere been defined as an acacian system (Dormer, 1945 *a*), and which is apparently the ancestral type for the Leguminosae.

PODALYRIEAE

This tribe, as at present constituted, comprises two very dissimilar groups, which have almost nothing in common as far as vegetative structure is concerned, and which may conveniently be distinguished as the northern and southern Podalyrieae.

(*a*) *Genera of the northern hemisphere*

The phyllotaxy is uniformly distichous, and the vascular systems always conform to a single pattern, a closed system with deeply interlocked trilacunar insertions (Dormer, 1945 *a*, fig. 1).

Considerable interest attaches to the morphology of the stipules in this group. In the woody genera of the Old World, *Piptanthus* and *Anagyris*, the stipules are deeply fused, so as to form a single structure which stands opposite the leaf, and which only reveals its double nature by being more or less notched at the tip. The vascular system of the stipules is continuous right round the node. In systematic works the stipules of the herbaceous genera *Thermopsis* and *Baptisia* are generally described as 'free', but actually the position is not quite so simple as this would imply. An examination of the aerial shoots of *Thermopsis montana* shows that there is a smooth transition from the leaves at or below soil level, which have their stipules fused for the greater part of their length, the lamina and petiole being hardly if at all developed, to the normal foliage leaves on the upper part of the shoot, where the union of the stipules becomes progressively less obvious. But it is only in the last leaf of all, the one that stands at the foot of the terminal inflorescence, that the stipules are genuinely free. In the other leaves the stipules are connected by a very shallow sheath, but this sheath contains a vascular bundle, so that here, as in the woody forms, there is a complete ring of vascular tissue girdling the node. A similar state of affairs is to be seen in *Baptisia australis*, though here several of the upper leaves have free stipules, and not just one as in *Thermopsis*. It has been shown by Hanstein (1858) that a complete girdle of vascular tissue at the node is not uncommon in species with opposite leaves, but this appears to be the first recorded instance of such a structure in forms with alternate leaves. The union of the stipules is probably related to the great width of the leaf-insertion in this group, a similar association between wide insertions and fused stipules being found in a number of other groups of Leguminosae, though it is only in these Podalyrieae that there is also a union between the vascular systems of the two stipules. Probably the presence of a complete ring of vascular tissue has had something to do with the development of the remarkable condition seen in *Baptisia perfoliata*, in which a broad lamina extends all round the stem at each node (Curtis's *Bot. Mag.* 3121).

It seems not unreasonable to conclude from the persistence of stipular fusion in the basal parts of the herbaceous forms that the fused condition of the stipules is primitive for the tribe as a whole. This interpretation is in accordance with a number of other facts. In the woody forms the flowers are borne in association with structures which can only be regarded as unmodified leaf-bases, the petioles and laminae of which have been suppressed. Many of the herbaceous types, on the other hand, have specialized bracts, which differ from the foliage leaves in their narrow insertions and spiral arrangement. The herbaceous types, and particularly some species of *Baptisia*, show signs of specialization in the leaf, both in the reduction of the leaflets to one and in the more or less complete suppression of the stipules, conditions which do not occur in the woody genera. Furthermore, it may be pointed out that if the woody forms are regarded as primitive, the origin of the group may be definitely located in the Old World, which is in harmony with the epulvinate condition of the series.

(*b*) *Genera of the southern hemisphere*

With only trifling exceptions, the members of this group are woody with polymerous phyllotaxy, and so far as is known the vascular systems are all open.

The South African species are all constructed on the acacian plan, with regular 2/5 spiral phyllotaxy and trilacunar nodes.

The Australian genera depart rather widely from the typical acacian scheme. Of ten species which have been examined in some detail no less than eight were found to be unilacunar, while two of the ten had distinctly verticillate phyllotaxy. Moreover, while a typical acacian vascular system shows in any transverse section about twelve or fifteen bundles, in these species a section may contain as many as forty distinct primary xylem groups.

It is clear that the southern Podalyrieae are to be regarded as acacian derivatives, the South African genera being fairly close to the prototype, while the Australian have diverged more widely from it. The suggestion by Reinke (1897) that the southern Podalyrieae are xeromorphic derivatives of the northern ones seems to be quite ruled out by the facts of vegetative structure. Much more fruitful is the idea (Andrews, 1914) that both groups are temperate offshoots of the tropical Sophoreae. So far as the southern types are concerned this view offers no special difficulties, but it is at present impossible to make any useful suggestion as to the origin of the northern genera. Perhaps the investigation of the few distichous Sophoreae will yield some relevant information. The northern genera appear to be rather specialized types, and if, as Compton (1912) supposes, the tetrarch type of seedling is the primitive one for the family, the constant diarchy of these genera is an additional reason for supposing that they do not occupy such a lowly position among the Papilionatae as the freedom of their stamens is commonly considered to indicate. The seedlings of the southern genera are tetrarch.

GENISTEAE

Although in many respects the members of this tribe show great diversity of structure, the overwhelming majority of them can be regarded without serious theoretical difficulty as modifications of the acacian scheme.

Lipariinae

So far as is known at present, all the members of this subtribe are polymerous and unilacunar. *Coelidium* and *Walpersia* differ from the other genera in that their stamens are monadelphous. They show greater specialization in the reduction of the number of seeds in the pod, and *Walpersia* also in the fusion of the stamen-tube to the bases of the petals. It is of interest that these genera are also distinguished by a strong tendency to become verticillate.

Bossiaeinae

The genera of this subtribe fall into two groups, as follows:

(*a*) Anthers alternately small versatile and large basifixed, phyllotaxy almost uniformly spiral: *Templetonia*, *Hovea*.

(*b*) Anthers all versatile and of uniform size, phyllotaxy mostly dimerous: *Bossiaea*, *Platylobium*.

It is clear that the phyllotaxy data tend to confirm the classification based on androecial structure. *Goodia*, which differs from the other genera in having trifoliolate leaves, has anthers which show a pronounced size difference, although they are all versatile. Its phyllotaxy is spiral, so that its affinities seem to be with *Templetonia* and *Hovea* rather than with the dimerous types.

Some species of *Bossiaea* and *Platylobium* have their leaves placed in superposed opposite pairs, an extremely rare arrangement.

CROTALARIINAE

This is a large group spreading all over the tropics and subtropics, but is fairly obviously of South African origin. Table 3 shows the great concentration of genera and species in that part of the world. A South African origin is also suggested by Table 4, which gives the average numbers of leaflets occurring in the Crotalarias of various countries (cf. Dormer, 1945*a*, Table 2).

Table 3

Distribution	Genera	Av. no. of species per genus
Confined to South Africa	11	25·6
Found in South Africa and also elsewhere	2	220
Not found in South Africa	6	3·2

Table 4

2·83	Transvaal, with Swaziland
2·83	Cape of Good Hope
2·72	Tropical Africa
2·68	Sudan
2·44	West Tropical Africa
2·43	City of Madras
2·00	Jamaica
2·00	Panama Canal Zone
1·80	Brazil
1·80	Orient
1·67	Australia
1·50	South-eastern United States
1·43	Ceylon
1·42	India
1·00	Canada and the northern United States
1·00	Palestine, Syria, and Sinai

Table 5

Phyllotaxy	Woody	Habit mixed	Herbaceous
Entirely polymerous	10	1	—
At least partly dimerous	—	1	2

On referring to Table 5, which is based on an examination of fourteen genera of the subtribe, it will be seen that there is a marked correlation between phyllotaxy and general habit. The geographical distribution of phyllotaxy and habit is such as to lend support to the presumption of a South African origin for the group. Of the six genera which are known to contain herbaceous species, only one is confined to South Africa, while three do not occur there at all. Of the three genera known to contain distichous species none is confined to South Africa and two do not occur there. The most specialized forms appear to be *Sellocharis* and *Anarthrophyllum*, in which the stipules are fused so as to form a sheath round the stem. The former genus is verticillate, the latter distichous, and both are South American. One may sum up the situation by saying that the more specialized species occupy a peripheral position with respect to the area of distribution of the subtribe as a whole, the primitive ones being concentrated about the centre of origin.

TRIFOLIEAE

In all the members of this tribe the stipules are clearly adnate to the petiole, and when the nodes are trilacunar, as is usually the case, the insertions are in contact. In other respects the group is a very variable one.

In the introduction to his monograph of the genus *Melilotus*, Schulz (1901), distinguishes two subtribes, one with the micropyle above the funicle, including *Ononis*, *Trifolium* and *Parochetus*, and one with inferior micropyle including *Melilotus*, *Medicago* and *Trigonella*. It is therefore of considerable interest to find that the genera of the *Ononis*-group are characterized by the fusion of the stipules to form a sheath encircling the stem, while in the *Trigonella*-group the stipules, though adnate to the petiole, are free from each other, leaving the side of the stem opposite the leaf naked.

There are other facts tending to support this classification. Thus, in the grouping of Leguminosae by cross-inoculation experiments (Waksman, 1927), *Trifolium* falls into one group, *Trigonella*, *Medicago* and *Melilotus* forming another. Although the character is not absolutely constant, it is worth noticing that the stems of the *Trigonella*-group are usually more or less prominently ridged or angled, whereas those of the other genera are smoothly cylindrical.

Table 6

Habit	No. of leaflets to each leaf		
	More than three	Three	Less than three
Woody	26·7	86·7	13·3
Perennial herbs	18·2	81·8	36·4
Annuals or biennials	2·3	83·3	41·7

The species generally known as *Trigonella ornithopodioides* is of particular interest in this connexion. It differs from all other species of *Trigonella* investigated in having its stipules fused into a conspicuous sheath, suggesting an affinity with the *Ononis*-group. This impression is confirmed by the fact that the micropyle is superior. It appears therefore that this is no *Trigonella*, but that it should either be included as an anomalous species of *Trifolium* or made the type of a new genus, in which case its proper name appears to be *Falcatula ornithopodioides* Bab.

The genera can be further distinguished, to a certain extent, by phyllotaxy. *Ononis* and *Trigonella* are variable, while *Melilotus* is regularly spiral, and *Trifolium* and *Medicago* constantly distichous.

Ononis affords one of the best examples of correlation between leaf-structure and general habit, as shown in Table 6, which is based on sixty-two of the sixty-seven species recognized by Širjaev (1932). The figures represent percentages of the total number of species of the same habit. It will be found that the sum of the percentages for a given type of habit is considerably in excess of one hundred. This is due to the fact that there are many variable species which enter the table in two or three columns. It is obvious that the proportion of species with more than three leaflets, decreases with increasing specialization of habit, while the proportion with less than three increases.

LOTEAE and HEDYSAREAE-CORONILLINAE

A number of systematists have suggested that these two groups may be related, and a study of the vegetative features appears to establish such an affinity beyond all reasonable doubt.

In both tribes the shoot is uniformly distichous with trilacunar nodes and a closed vascular system. In most cases there is only a single stem bundle between the median trace of a leaf and each lateral trace.

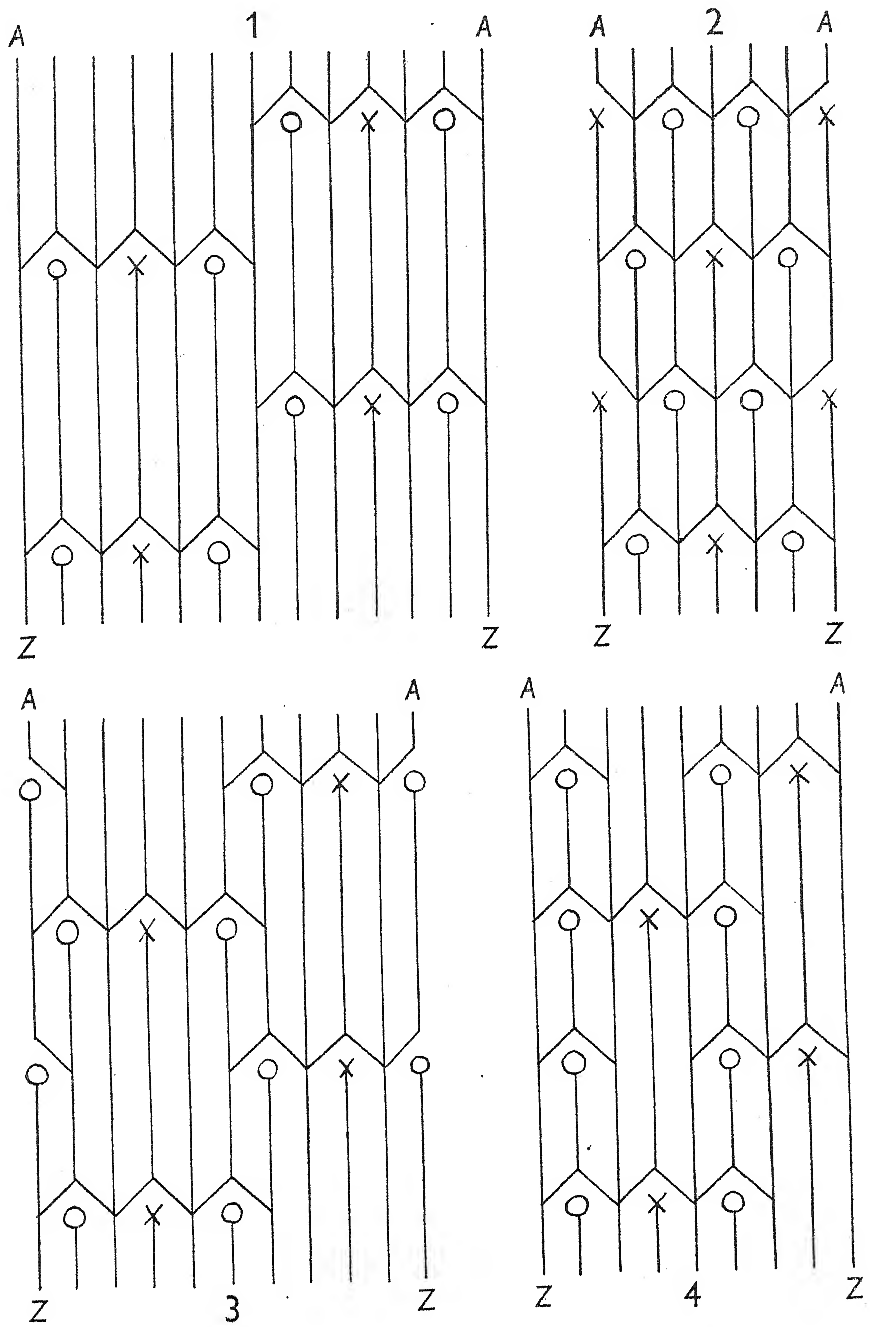
Obviously, the number of possible types of vascular system conforming to this specification is severely restricted. As long as the two rows of leaves are diametrically opposite,

Table 7

Loteae	
Lotus tetragonolobus	12-fold
L. corniculatus	12-fold
Dorycnium suffruticosum	12-fold
D. rectum	12-fold, but with extra bundles
Securigera coronilla	9-, 10-, 11-, or 12-fold
Anthyllis vulneraria	12-fold, but with extra bundles
Hedysareae-Coronillinae	
Coronilla, section *Emerus*	
C. emerus	12-fold
Section *Eucoronilla*	
(*a*) Species with free stipules:	
C. varia	12-fold
C. cappadocica	8-fold
(*b*) Species with stipules fused, though not so deeply united as to be so described in systematic works (e.g. Coste, 1901)	
C. glauca	8-fold
C. valentina	8-fold
C. juncea	Anomalous, see text
(*c*) Species with stipules deeply fused, and generally admitted to be so by systematists:	
C. minima	6-fold
C. vaginalis	6-fold
C. coronata	Anomalous, see text
Section *Scorpioides*	
C. scorpioides	8-fold
Ornithopus sativus	12-fold
O. compressus	10-fold or 8-fold
Hippocrepis comosa	8-fold
H. multisiliquosus	12-fold

only four simple layouts appear to be conceivable (Figs. 1–4). In these figures the stele is represented as though it were cut open down one side and then laid out flat. Crosses denote median traces and small circles laterals. The bundles lettered *AZ* have been represented twice over in each diagram.

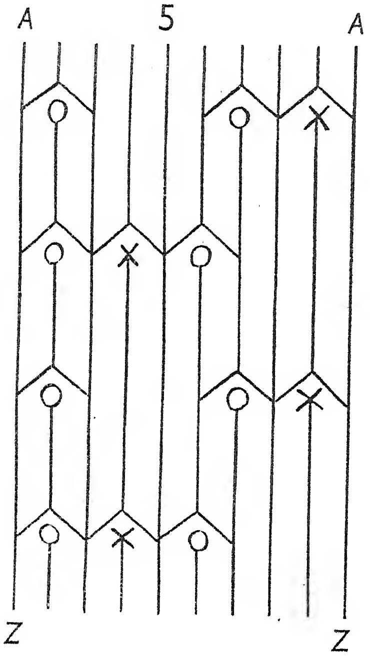
These patterns differ in the number of bundles traversing the internodes, so that the various types may be specified as 12-fold (Fig. 1), 10-fold (Fig. 3), and so on. All these vascular patterns actually exist, and they are characteristic of particular species in the same way as are chromosome numbers. The known examples are listed in Table 7. Further possibilities arise when the two ranks of leaves are no longer strictly opposite, so that the shoot is more or less dorsiventral. Fig. 5, for example, shows a 9-fold system, the 7-fold and 11-fold analogues of which are too obvious to require illustration. The members of this series apparently occur only as rather infrequent abnormalities, and the existence of the 7-fold pattern is somewhat doubtful, though it could probably be found

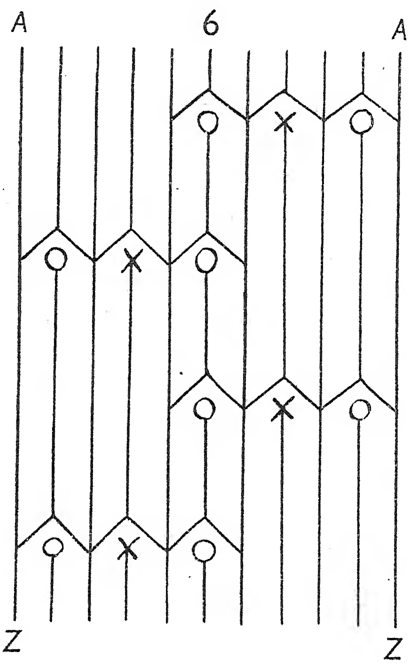


Figs. 1–4. In these diagrams the stele is represented as though cut open down one side and then laid out flat. Crosses denote median traces and small circles lateral ones. Fig. 1, 12-fold vascular system of the Coronillinae; Fig. 2, 6-fold system; Fig. 3, 10-fold system; Fig. 4, 8-fold system. In each case the bundle lettered *AZ* has been drawn twice over.

if searched for. Finally, we must consider the arrangement shown in Fig. 6, a 10-fold system with pronounced dorsiventrality. This pattern occurs constantly in the genus *Scorpiurus*, but is not known elsewhere.

The distribution of the various patterns among the species is of great phylogenetic interest, particularly when taken in conjunction with other characters. It is usual for all the shoots of a species to conform to the same pattern. Thus a number of plants of *Ornithopus sativus* has been examined without finding any exception to the 12-fold plan shown in Fig. 1, while the vascular system of *Coronilla scorpioides* is as regularly 8-fold, according to Fig. 4.





Figs. 5, 6.

Fig. 5. A 9-fold vascular system, occurring only as an uncommon departure from the normal.
Fig. 6. Dorsiventral 10-fold system characteristic of the genus *Scorpiurus*.

Two species, *Ornithopus compressus* and *Securigera coronilla*, are exceptions to this rule, and perhaps give an indication of the way in which the change from one pattern to another may have come about in the course of evolution. In *Securigera*, of which a considerable quantity of material has been available for investigation, 9-, 10-, 11-, and 12-fold symmetry has been observed. In all cases, a given axis preserves the same type of structure from the time of its origin as an axillary bud to the cessation of its growth. In other words, the shoot-apex simply repeats a pattern an indefinite number of times, but is not capable of changing from one pattern to another. On the other hand, the various shoots of an individual exhibit different patterns; one shoot, for example, had an 11-fold vascular system, while its axillary buds were 10-fold and 12-fold in about equal proportions. The available information suggests that in this species the 10- and 12-fold systems are about equally common, while the 9- and 11-fold are relatively infrequent. An essentially similar state of affairs seems to exist in *Ornithopus compressus*, where both

8-fold and 10-fold systems have been seen. It is probable that further investigation would reveal similar variability in other groups, and it is already clear that a comparable phenomenon occurs in some species of *Trifolium*. Thus of two shoots of *T. pannonicum*, taken from the same plant, one had twenty bundles in each internode, the other seventeen. It seems reasonable to conclude that changes from one type of symmetry to another have always been accomplished suddenly. There is nothing to show that intermediates ever existed, nor, from the nature of the case, is it easy to imagine a gradual transition.

Reference to the figures will make it clear that the smaller the number of bundles in the stem, the greater is the fraction of the circumference occupied by the insertion of each leaf. If the width of the insertion is measured in degrees of arc, which was the mode of expression adopted by Naegeli (1858), and if the bundles are assumed to be equidistant, the widths for 12-, 10-, 8-, and 6-fold systems are respectively 120, 144, 180 and 240°. It will be shown that these differences are associated with conspicuous modifications of the stipules.

The application of these principles may best be illustrated by a discussion of the genus *Coronilla*. Three sections are recognized in systematic works, and are best treated separately.

Emerus contains two species, *Coronilla emerus* and *C. emeroides*. Both are shrubs with 12-fold vascular systems. The leaves are pinnate with numerous leaflets, and the stipules are free—that is to say, they show no tendency to form a sheath round the stem.

It has been possible to examine eight species of *Eucoronilla*. The stipules are free in some species of this section, more or less fused in others, differences which may conveniently be expressed by dividing the species into three groups, as has been done in Table 7.

In the anomalous species *Coronilla juncea* and *C. coronata* the number of bundles in a transverse section of the stem greatly exceeds the figures for the other species, and a lateral trace is separated from the corresponding median trace not by a single bundle but by several. In both species it appears that the lateral traces of successive leaves are superposed, which, as reference to the figures will show, is the arrangement found in 8-fold systems. The marked increase in the number of bundles in these species is probably due to the interpolation of new bundles between those of the original system. Some indication of such a process may be seen in the stronger shoots of *C. varia*, in which very small subsidiary bundles sometimes run between the main bundles which mark out the 12-fold system characteristic of the species.

Eucoronilla comprises both shrubs and herbs, and is therefore rather more specialized with regard to habit than the purely woody section *Emerus*. This greater specialization is shown also in the fusion of the stipules in many of the species, and in the wider insertion of the leaf with which this fusion is closely associated.

Scorpioides, the last section, consists of three species, all annual herbs, with deeply fused stipules. The only species examined, *Coronilla scorpioides*, has an 8-fold system. There is a marked reduction in the number of leaflets to a leaf.

It is clear that the genus *Coronilla* exhibits a fairly regular transition from woody forms with free stipules and 12-fold vascular systems to annual herbs with deeply fused stipules and 6-fold or 8-fold vascular systems. A somewhat similar, though less complete, series appears to exist in the allied genus *Hippocrepis*, where *H. multisiliquosus* has a 12-fold system and free stipules, and *H. comosa* an 8-fold system and fused stipules.

Except for *Securigera*, all the Loteae examined conform fairly closely to the 12-fold plan, though in *Anthyllis* and some species of *Dorycnium* there is a tendency to increase the number of bundles, as in *Coronilla juncea*.

The study of the vegetative shoot in the two groups under consideration leaves a strong impression of similarity, an impression which a review of the principal floral characters tends to confirm. In both tribes the flowers are arranged in umbels and show a strong tendency to the development of the type of pollination mechanism seen in *Coronilla* and *Lotus*, in which a thread or ribbon of pollen is driven out of the pointed carina by the swollen filaments of the antesepalous stamens (Knuth, 1908). The chromosome numbers are also in accord, each series showing a tendency to reduction from 8, which is the basic number most usual in the epulvinate Papilionatae (Senn, 1938). Geographically, the two tribes agree in being centred on the Mediterranean basin, though with considerable extensions beyond it. It is well known that in *Lotus* and *Dorycnium* there are regularly five leaflets, the lower pair being so close to the stem as to resemble stipules, the true stipules being vestigial or absent. An approach to this condition is to be observed in *Ornithopus compressus*, *Coronilla minima*, *C. varia*, *C. scorpioides*, and *C. coronata* among the Coronillinae.

Conclusive evidence as to the relationship of the two tribes appears to be supplied by a study of the seedlings. It has elsewhere been shown (Dormer, 1945*b*) that in *Securigera* and *Scorpiurus* among the Coronillinae and in *Lotus tetragonolobus* there is no plumule, the entire epicotyledonary part of the plant being produced from the axillary buds of the cotyledons. This condition is not yet known in any other plants whatever; perhaps the closest known parallel is in *Welwitschia*, though in the gymnosperm the plumule does produce two leaves before its apex aborts, whereas in these Leguminosae there is never any vestige of the plumule. It is noteworthy that in the forms without a plumule there is a strong tendency to the development of more or less conspicuous wings or ridges on the pod, structures which do not occur in the species with normal seedlings. In *Scorpiurus*, as is well known, the legume has nine or ten longitudinal ridges, each associated with a vascular bundle (Saunders, 1929). It is less generally realized that the two slight ridges along the vexillary margin of the pod of *Securigera* are also provided, in many specimens, with a definite vascular supply. *Lotus tetragonolobus* differs from others of the genus in having four broad wings running along the legume; these wings are not associated with special longitudinal vascular strands, but are in other respects comparable with the ridges of the two genera mentioned above.

It may therefore be suggested that the Loteae and Coronillinae should be combined, the group so formed being subdivided into a series with winged or ridged pods and a seedling without a plumule, and a series with plumules and normal pods.

GALEGEAE

It has already been pointed out that this tribe contains both pulvinate and epulvinate genera. It is, in fact, a heterogeneous assemblage of all those Papilionatae which lack characters sufficiently striking to lead to their being placed in any other tribe.

Indigoferinae

Several species of *Indigofera* have been examined. All are trilacunar, with open vascular systems and insertions in contact.

It can be shown that in this genus there is a marked correlation between phyllotaxy and general habit. Of seventy-three species which have been examined, nineteen were herbaceous, the remainder more or less shrubby. Of the shrubs, eighteen, or 33%, showed distichous phyllotaxy, the remainder being spiral. Of the herbs, on the other hand, no less than seventeen, or 90%, were distichous. Reference to Table 8 will show that there is also a distinct relationship between habit and the form of the leaf, the woody species having a higher number of leaflets to a leaf than the herbs.

Psoraleinae

This is a pulvinate series confined, except for some species of *Psoralea* itself, to the New World. *Dalea mutisii* has a typical acacian system, while in *Petalostemon* there are eight stem bundles and 3/8 spiral phyllotaxy, and the lateral traces run some distance as cortical bundles. In various species of *Psoralea* there is a tendency to the separation of the insertions, and in *Amorpha* the insertions are always widely separated, and the phyllotaxy sometimes becomes irregular.

Table 8

Country	Av. no. of leaflets per leaf		
	Shrubs	Subshrubs	Herbs
India	9·43	4·43	3·89
South Africa	5·27	5·75	4·41

These facts can be correlated, to a certain extent, with what is known of the group from the floral side. *Dalea* has a generalized type of flower, and the reduction of the number of seeds in the pod, which is a pronounced characteristic of the subtribe, is not carried so far as in the other genera. *Psoralea* shows advance in the reduction of its seeds to one, and of its leaflets, in most cases, to three or one. *Amorpha* has a corolla reduced to a single petal, while in *Petalostemon* there are only five stamens. It is reasonable to suppose that the acacian structure of *Dalea* represents the ancestral condition for the group. According to Allen (1882), the fact that *Dalea* is the only genus known to produce yellow flowers would be an additional reason for regarding it as primitive.

It can be shown that in the genus *Psoralea* the American species have, on the average, a higher number of leaflets per leaf than the species of the Old World. This, of course, is consistent with the American origin of the genus, and therefore also of the group as a whole.

Psoralea orbicularis is of interest as it has a closed vascular system, distichous phyllotaxy, and interlocking trilacunar insertions. This species and *Arachis hypogeaea* are the only pulvinate Papilionatae so far known to have closed vascular systems.

Tephrosiinae

Galega differs from the rest of the subtribe in being epulvinate. It has a closed vascular system with rather wide trilacunar insertions, and its whole morphology is entirely in harmony with its epulvinate condition. As far as vegetative features are concerned, one would tend to compare *Galega* with *Astragalus* rather than with any pulvinate form.

Millettia pulchra, *Wisteria chinensis* and *Peteria scoparia* have spiral phyllotaxy, open vascular systems, and separated trilacunar insertions. Several species of *Tephrosia* have

been examined, and all were found to have distichous phyllotaxy with interlocking trilacunar insertions. In this genus there is a distinct correlation between leaf-form and habit. Taking the South African flora as an example, the species described as shrubs have, on the average, 14·3 leaflets per leaf, the subshrubs 8·4, and the herbs 5·0.

ROBINIINAE

The members of this subtribe, so far as they have been investigated, are trilacunar with open systems. The species of *Robinia*, *Coursetia*, *Cracca* and *Sesbania* mostly have spiral phyllotaxy, their insertions being in contact or slightly separated. There are in addition a number of distichous genera, and the distribution of these is of considerable interest. The group is predominantly American, and is therefore probably of American origin. It is worthy of note that all the distichous genera are found outside the American continent, and that most of them show pronounced reduction of the leaf. *Microcharis* has simple leaves and occurs in Africa, while *Carmichaelia*, *Notospartium* and *Streblorrhiza* are endemic, the first two to New Zealand and the latter to Norfolk Island. *Carmichaelia* and *Notospartium* are typical switch plants, and in the former, at any rate, the separation of the insertions is carried much farther than in any of the forms with normal leaves.

Table 9

Av. no. of flowers	No. of species	Av. no. of leaflets
1·0– 2·5	3	8·0
3·0– 4·5	6	10·2
5·0– 6·5	1	11·0
7·0–10·0	1	22·0

Table 10

No. of flowers	No. of species	No. of leaflets
3 or 4	1	12·0
1 or 2	4	9·5
1	14	6·4

COLUTEINAE AND ASTRAGALINAE

A partial account of these two series has already been given in a previous paper (Dormer, 1945*a*, p. 146). They have in common a type of leaf-base in which the stipules are joined by a narrow commissure which forms a sheath across the abaxial face of the petiole. Such a structure does not occur in any other Leguminosae, and there can be little doubt that the two groups are closely allied.

The species of *Colutea* have small axillary inflorescences, each bearing a few flowers. It sometimes happens that the flower is solitary in the axil of the leaf, in which case the pedicel is always distinctly jointed about halfway up. This seems to indicate that the solitary flower results from the reduction of a several-flowered inflorescence. It is therefore of interest that there is a correlation between the number of flowers in an inflorescence and the number of leaflets in a leaf (Table 9). It seems necessary to suppose that in this genus there has been a progressive reduction of the inflorescence together with a corresponding reduction of the leaf.

Caragana differs from *Colutea* mainly in the suppression of the terminal leaflet and in the spinous development of the stipules, and sometimes also of the persistent rachis of the leaf. It is therefore natural to regard *Caragana* as a more specialized genus, and this seems to be confirmed by the fact that, as shown in Table 10, it is possible to demonstrate a similar correlation between inflorescence and leaf to that already seen in *Colutea*, but that the numbers, both of flowers and of leaflets, are smaller than in that genus.

It has already been pointed out that *Glycyrrhiza*, which is placed by systematists in the Astragalinae, differs from the rest of the subtribe in being pulvinate. In *Glycyrrhiza* there is an open vascular system with separated trilacunar insertions. Separated insertions do not occur in the other genera of the subtribe, most of which, furthermore, have closed systems. *Astragalus* has a closed system with interlocking insertions, both in the spiral and in the distichous species. *Glycyrrhiza* is further characterized by the possession of peltate hairs and pronounced secretory activity—in fact its vegetative morphology is wholly typical of pulvinate forms in general, and entirely opposed to its inclusion in the Astragaline. Possibly there may be some affinity with the Psoraleinae—certainly the inflorescences are very similar.

HEDYSAREAE

Like the Galegeae, this is undoubtedly an unnatural tribe, and the subtribes need to be redistributed among the other groups of Papilionatae. It has already been shown that the Coronillinae should be placed with the Loteae, but so far it is possible to make a useful suggestion as to affinity in only one other subtribe.

Desmodiinae

The morphology of the shoot in the genus *Desmodium* has already been discussed (Dormer, 1945*a*, p. 148), and has been shown to be consistent with the hypothesis of an American origin for the genus. The Desmodiinae, however, have the greater number of their genera and species in the Old World, as indicated in Table 1 of the present paper. It is of interest that a transverse section of the stem of *Lespedeza sieboldi*, with widely separated trilacunar insertions, irregular polymerous phyllotaxy, and a peculiar close-packed arrangement of the bundles in the stem, is indistinguishable from a similar section of a species of *Amorpha*, among the Psoraleinae. No other Papilionatae are known to exhibit precisely this type of structure. The resemblance may be more than coincidence, and it is at least suggestive that the basic chromosome numbers in Psoraleinae and Desmodiinae are the same, and that Watari (1934, p. 284) comments on the similarity of the petiolar structure of *Amorpha fruticosa* to that of *Lespedeza*. The reduction of the corolla which is so marked a feature of *Amorpha* has been carried even further in some species of *Lespedeza* which are apetalous, and both groups show similar reduction of the number of seeds in the pod.

It may therefore be tentatively suggested that the Desmodiinae have been derived from the Psoraleinae, and that both series are descended from an American ancestry. If the two subtribes are combined, the resulting aggregate has most of its genera and species in the New World, as one might expect. Further support for this view can be obtained from Tables 11 and 12, of which the former represents the distribution of various types of habit among the genera of Desmodiinae, while the latter shows in the same way the distribution of phyllotaxy in this group. Both tables indicate that the forms occurring in

the Old World are more specialized than the American ones. The Desmodiinae are the only known group of Papilionatae in which the indications of tables of this kind conflict with the results of comparing the numbers of genera and species in different countries.

Aeschynomeninae

The majority of the members of this group are American. There is a strong correlation between phyllotaxy and habit, as shown in Table 13. In Table 14 are set out the statistics of habit for the various genera, scoring a genus twice when its habit is variable. The figures have been reduced to percentages. This table shows clearly that the forms of the Old World are, on the average, more specialized than the American ones, which is entirely consonant with the presumed American origin of the group.

Table 11

	Herbaceous	Mixed	Woody
Old World	5	6	3
New World	—	2	1

Table 12

	Distichous	Mixed	Spiral
Old World	3	1	2
New World	—	1	1

Table 13

	Woody	Mixed	Herbaceous
Polymerous	3	1	—
Mixed	—	2	2
Dimerous	—	—	2

Table 14

	Trees	Shrubs	Herbs
New World	8	59	33
Both hemispheres	0	50	50
Old World	0	40	60

DALBERGIEAE

A predominantly American series, pulvinate, and entirely woody. The vascular systems are all open, and in the trilacunar forms, which are greatly in the majority, the insertions are always separated.

Pterocarpinae

Several members of this group have been examined. All have exactly the same type of structure—a distichous shoot with trilacunar insertions which are not directly opposite, so that the shoot is somewhat dorsiventral.

Geoffraeinae

Constantly spiral, and some of the species multilacunar.

Lonchocarpinae

Phyllotaxy variable, nodes sometimes multilacunar.

VICIEAE

The true Vicieae, that is to say all the genera except *Abrus*, have a very uniform type of structure, with trilacunar nodes and a closed vascular system, the insertions being in contact, and the lateral traces, except in *Cicer*, running down one internode as cortical bundles.

It has long been recognized that *Abrus* differs very markedly from the rest of the tribe. It is pulvinate, spiral, and woody, with an open vascular system. It has a number of features, such as anomalous secondary thickening, opposite first leaves in the seedling, and basic chromosome number 11, which are typical of pulvinate forms in general, and which, of course, do not occur in the other genera of Vicieae. The morphology of *Abrus* is such as to confirm an impression already widespread among systematists, that it should occupy a place near the Phaseoleae and Dalbergieae.

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REVIEWS

Marine Algae of the Monterey Peninsula, California. By GILBERT M. SMITH, Professor of Biology, Stanford University. Published by the Stanford University Press, Stanford University, California. Oxford University Press. London: Humphrey Milford. Price 36*s.* net.

The book comprises a short introduction of 14 pages; a glossary; 412 pages of text; a series of 98 plates in which beautiful draughtmanship, artistic arrangement and scientific accuracy are admirably blended; a bibliography and an index.

The subject-matter is largely based on seventeen years of personal collection of algae from one area, that of the Monterey Peninsula on the coast of California; an area large enough to represent adequately the whole western coastline, yet small enough to be covered in detail by a competent and persistent algologist. Prof. Smith, himself emphasizes the value of the chosen area by pointing out that it includes in its flora 80 % of the algae reported for the whole coastline from Puget Sound to Southern California, and is itself the type region for 25 % of the west coast flora.

Though personal observation of the field has contributed largely to the making of the book, contemporary and earlier work on the same area has been carefully studied and its contribution to the subject embodied in the text.

The book is quite frankly a systematic list in which each specimen is described with the strictest economy of space. The locality and details of the habitat of each specimen is indicated only by reference to its bathymetric zone and to the particular locality in which it is to be found, or from which it has been recorded. The description is limited to a condensed statement of the features essential for justifying its systematic position, and an indication of the nature of its reproductive mechanism.

To condense such treatment of 405 species into a volume of reasonable size and price, calls for strict economy and permits of skeletal description only.

The purpose of the book, apart from the establishment of a record of the flora of the area, is clearly that of providing students of algology on the west coast of America with a means of identifying their finds. For this purpose keys are clearly essential. In composing them, Prof. Smith has borne in mind the needs of unspecialized students, and provided for them by introducing at the end of the book, comprehensive keys based on external features, or others which a student may readily identify. The detailed keys heading the various subdivisions of a phylogenetic arrangement are based on characters less readily determinable and often relating to features of reproduction on which systematic classification may be based. The needs of students are further catered for by the Introduction, in which some space is devoted to methods of collection, preservation and mounting.

This consideration for the needs of non-specialist students is welcome, for it is often insufficiently considered by writers of handbooks. The entry of a student into such a field of botanical study as that of algology can be made only by the initial step of ability to identify material with certainty. Keys based on characters of systematic value may prove useless to the inexperienced. Of what value or use is an 'alternative' referring to gametophytic characters if the student has in his hands a sporophytic specimen? The question of size is more important than it might seem at first sight. Type descriptions are based usually on newly discovered specimens, but there is no guarantee that the type specimen is really typical of the species. From this point of view the keys in the book are well devised. Size in the algae is a peculiarly elastic feature and differs markedly from one locality to another and even from level to level within one restricted area. Only personal collection from many localities will give proper appreciation of the size-range for any given species. From this point of view the keys in this book are well devised.

To counteract the evil effects of too great condensation, the author has made full use of original descriptions by other writers, and where these are lacking in detail, or where new knowledge has emphasized the importance of features not included in the original description, Prof. Smith has filled in the lacunae from his own first-hand knowledge. Only those who have worked extensively in the field know how imperfect a type description from older publications may be when applied to specimens outside the type area.

Prof. Smith deals only with the Chlorophyta, Phaeophyta and Rhodophyta of his area. All other groups of algae are left untouched.

Comprehensive treatment of an ever-growing number of genera and species entails increasing concentration on one or other aspect of study to the exclusion of the rest, if the published results are not to exceed well-defined limits of size and cost. In a systematic treatise, description must be reduced, so to speak, to its lowest terms. A purely systematic treatment has the disadvantage of depriving the would-be algologist of a great deal of information about his material which would be valuable to him. In the present publication there are omissions which detract from its usefulness to a student. The ecological aspects of the area; the interaction of one plant with another; seasonal behaviour; the question of annual and perennial habit, for example, are aspects of algology to which the minds of students should be directed. They are not discussed at all. Doubtless the omission is deliberate, but one deplores the inference which a student may, perhaps unconsciously, make that a species is fully understood when its systematic position is accurately determined. Conception of an alga as a unit in a scheme of classification rather than as a living organism reacting to the specialized environment of the sea, is an attitude of mind only too readily adopted by the student, and one which tends to close the door in the face of a possible entrant into an interesting and valuable field of research.

Prof. Smith's careful integration into the text, of bibliographic reference for each species does something to mitigate this deficiency, but one cannot help wishing that the author had taken this opportunity of sharing with his algological public the full wealth of biological knowledge of the algae which he must have collected in the course of his studies in the field. M. KNIGHT

The Pleistocene Period: its Climate, Chronology and Faunal Successions. By FREDERICK E. ZEUNER, D.Sc., F.Z.S., F.G.S. $5\frac{1}{2} \times 8\frac{3}{4}$ in. xii+322+7 pp. 76 figs. The Ray Society, London. 1945. £2. 2*s*.

The value of this book, which in the main is concerned with the establishment of an absolute chronology for the Pleistocene period, depends on the approach to it. A critical reader may be stimulated, for there are definite points of view confidently presented and maintained with some show of support. Sources are liberally given (the bibliography occupies 26 pages); not only those supporting the author's thesis but many contrary authorities and general references are cited. There are, however, some unexpected omissions. In the hands of a reader too ready to accept the author's determinations and to build further theories on them the book may be a positive danger. The more one considers the questions raised the more certain one becomes that there is not yet available enough evidence to decide for or against the author's interpretation of Pleistocene chronology, and the more doubtful one becomes of the wisdom of offering, at this stage, so complete a theory.

The first chapter is a good brief account of the principles of Pleistocene stratigraphy, the value of which would have been still greater had it been a little expanded and better illustrated. This is followed by an excellent description of the formerly glaciated and the periglacial areas of continental Europe, an admirable survey in which the author's wide knowledge of the literature and of the terrain is well used. His conclusions are arrived at by careful consideration of many opinions. The area lends itself to a study of this type because the stratigraphy has been well worked out and because the nature of the country, with long valleys extending from the glaciated areas to the periglacial zone, enables good connexions to be made.

The account given of the glaciation of the British Isles is less satisfying. The discussion of the East Anglian drifts, which is carefully summarized, is left in the air because the glaciation of the rest of England, of Wales and of Ireland (Scotland is not mentioned) is so superficially treated. It may be that it is not yet possible to trace the origins of the various ice-sheets, but the author certainly does not make the attempt. In his European section there is a good account of the terraces of the Somme and a full and detailed summary of the Pleistocene history of the Thames basin.

Although the discussion of the European problems may be uneven it is comprehensive, but the account of the North American Pleistocene occupies only two pages. The careful consideration of the periglacial area of the south of England leads to a cautious correlation with the East Anglian drifts whereas we find all the North American glaciations equated to events in Europe with no

adequate presentation of evidence. Such violent contrasts in treatment, of which there are more than one, are a serious fault.

Chapter five, a useful account of the astronomical theory, introduces formally the main thesis of the book, already obvious in the earlier parts. This, as has been said, is an attempt to prove an absolute chronology for the Pleistocene, based on the solar radiation curve. Dr Zeuner devotes about half the book to this. He weighs the evidence for and against, but he is so obviously ready to accept the absolute chronology that his judicial attitude is unconvincing. Those struggling with the details of Pleistocene stratigraphy and correlation will not feel comfortable at being confined within a ready-made framework. Perhaps they will not readily give consideration to a theory which cannot yet be proved, if ever it can, so they may well be grateful for so able a summary of the case.

After two chapters devoted solely to astronomy and chronology the author describes in detail the climatic phases in the Mediterranean area and briefly sketches an account of tropical Africa, South Africa, Antarctica, etc.

Into the general discussion of absolute chronology is fitted that of Pleistocene fluctuations of sea-level, which involves a world-wide correlation of ancient shorelines. In this too much weight is given to what may easily be chance correspondence in level at widely separated points. Some of the areas referred to in the discussion are zones of considerable seismic activity. When one combines an absolute chronology derived from theoretical considerations of astronomical matters with a sea-level controlled partly by the incalculable masses of the Pleistocene ice-sheets and partly by a hypothetical subsidence of the ocean floor, as is done in Fig. 76, what fantasies one can weave!

It is surprising to find no discussion of the effects of isostasy. The Baltic area and that of the Great Lakes of North America surely give clear enough evidence of the mobility of the earth's crust during the Pleistocene, yet the author ignores the possibility of any isostatic movement along the shores of the English Channel, for example, although the sea-level is said to have varied from plus 100 to at least minus 100 metres. And there is the still wider question: what amount has been eroded from the surface of the land during the half million years or so of the Pleistocene, and how much of it has been compensated by isostatic uplift? These movements may have had a great effect on the slopes of the rivers and until this effect is thoroughly examined inferences from the slope of Pleistocene river benches and from the levels of Pleistocene beaches are without much meaning.

The concluding chapter is an interesting attempt to establish a 'time-rate' for faunal evolution during the Pleistocene. The mammals and the land and fresh-water Mollusca are brought under review. Detailed lists are given and a few suggestions, the tentative nature of which are stressed by the author, are made. But the duration of the period is not long enough to observe such developments, as the author concludes that half a million years, practically the whole of the Pleistocene, would be a short time for the development of a new species.

It is a pity that preoccupation with the major climatic fluctuations, which may be fitted to the solar radiation curve, diverts the author from consideration of the more delicate variations which have been determined, for inter-glacial and late-glacial times, by examination of the flora. Late-glacial deposits are not described at all and only passing mention is made of inter-glacial floras.

There are many good things in the book but much of it is superficial which throws the whole work somewhat out of balance. There would have been less incentive to criticize had the book been given another title; for what sets out to be an objective account of a geological period slips rapidly into a sustained effort in special pleading.

A. FARRINGTON

Experimental Studies in the Nature of Species. Vol. II. *Plant Evolution through Amphiploidy and Autoploidy, with examples from the Madiinae.* By JENS CLAUSEN, DAVID D. KECK and WILLIAM M. HIESEY. 10×7 in., vii + 174 pages, 4 plates, 82 text-figures. Carnegie Institution of Washington, Publication 564. Washington, D.C. 1945. Price $1.25 paper, $2.00 cloth.

In Volume I of this series the authors (a cytogeneticist, an ecologist and a taxonomist) presented the results of studies of North American plants, establishing the pattern of variation within a number of species and subspecies, largely on the basis of extensive transplant experiments. In Volume II, they focus attention on the wider subject of evolution in groups of species; the data provided by experimental taxonomy are applied to the problem of evolution, and the term 'biosystematics' is coined to denote the new branch of science which is brought into view.

The authors begin with a description of their work in the Madiinae, a subtribe of the Compositae. They have produced artificially three amphiploids (more familiarly known as allopolyploids) in this group. Perhaps the most interesting is *Madia citrigracilis*, a rare Californian endemic, which was not discovered until a chromosome survey of *Madia* revealed that it was the only hexaploid in the genus, with $n=24$. *Madia gracilis* ($n=16$) and *M. citriodora* ($n=8$) were selected as likely parents, and crossed; the F_1 was highly infertile, but on selfing it gave, by gametic doubling, a small number of amphiploid plants. Successive generations showed increasing fertility and chromosome stability, and the final product was practically indistinguishable from wild *M. citrigracilis*.

The remainder of the volume is taken up with a valuable and detailed review of recent work on experimentally produced polyploids, and on the ecological characteristics of natural amphiploids and autoploids (= autopolyploids), some forty genera being treated in detail. Four 'biosystematic' units are proposed, which form the threads running through the account and linking the data in a coherent evolutionary scheme. The names of the units are borrowed from Turesson and Danser and are to some extent redefined; they are the ecotype, the ecospecies, the coenospecies and the comparium. According to the definitions hybridization between the members of different comparia is impossible, as is also gene exchange between members of different coenospecies. Thus the genera *Brassica*, *Raphanus*, *Sinapis*, and *Eruca* all belong to a single comparium, as they are linked by hybrids. *Madia citriodora* and *M. gracilis* would belong to different coenospecies were they not known to be linked by the amphiploid *M. citrigracilis*; they thus become ecospecies of a coenospecies. The four units are considered to represent stages in the evolution of the flowering plants; ecotypes represent the first stage of speciation. In time, these become ecospecies, coenospecies and eventually comparia, as genetical isolation becomes more and more marked. Autoploidy is regarded as arising at the ecotype level and as producing less diversity than amphiploidy, which occurs most typically after an inter-coenospecific cross, and reunites the 'diverging' branches for a time. When the limits of polyploidy are reached, the species may be given a new lease of life by the incidence of apomixis.

Most of the ideas which underlie this scheme are not found here for the first time, but they are stated with much cogency, and are applied in such a way that the data are linked clearly and systematically. The volume is, of course, a treatise on polyploidy, but the point is perhaps not made clearly enough that polyploidy is only a part of the evolutionary story of the flowering plants, and that we have, as yet, cytological knowledge of only a fraction of the flora of the world. It would not appear that the evolution of families and genera took place via polyploidy; rather it would seem that polyploidy is a mechanism which has favoured the rapid production of species by the adaptive radiation of genera into series of habitats. Polyploidy is thus seen as an evolutionary cul-de-sac; if the main line of evolution is to continue, the successors of the flowering plants will come from the non-polyploid groups of the present day. Such a group, the genus *Aquilegia*, is described by the authors; most of its members have $n=7$ and there are no strong barriers to interbreeding between them. The authors regard it as a 'youthful' genus from the evolutionary point of view.

With practical day-to-day taxonomy the scheme of Clausen, Keck and Hiesey has little to do; thus, well-marked taxonomic species which are interfertile may be classed as mere ecotypes while an autoploid which is practically indistinguishable from its diploid parents may be given ecospecific rank. Such a situation is inevitable when the classification is based mainly on a single criterion, in this case, a genetical criterion; but when the immense field of 'biosystematic' research has been thoroughly explored, a task as yet barely begun, new taxonomic arrangements and new nomenclature will have to be devised.

The volume may be summed up as a clearly written and stimulating monograph, meriting widespread attention and careful study.

D. H. VALENTINE

Hayfever Plants, their appearance, distribution [and] time of flowering and their role in hayfever with special reference to North America. By ROGER P. WODEHOUSE, Ph.D. $6\frac{3}{4} \times 10\frac{1}{4}$ in. Pp. xix + 245, with frontispiece, 71 figures and 10 tables in the text. Cloth. Waltham, Mass., U.S.A. The Chronica Botanica Company: London, Wm. Dawson and Sons, Ltd. 1945. $4.75.

The original discovery that hay fever is caused by the inhalation of air-borne pollen was made in England, but it has been exploited much more thoroughly in America. Studies made there during the past 30 years have shown that those pollens which are likely to be of clinical importance

in a given region must answer certain requirements: they must contain a specific substance (antigen) capable of evoking an allergic reaction, they must be buoyant, they must be produced in large quantities, and they must be of wide occurrence. These requirements are met in the main by the commonest anemophilous plants in the area: the pollens of some such species it is true, like those of the pines, contain no antigen and so may be disregarded; on the other hand widely occurring species which are only in part anemophilous (amphiphilous plants, as Wodehouse calls them) may, like privet in parts of the U.S.A., be an important cause of hay fever, but the general rule remains unaffected thereby. The contributions which botanists may make to this branch of medicine are therefore obvious: their part is to list the chief plants whose pollens are air-borne, to study and describe their pollens, to determine by appropriate methods in what quantities those pollens are produced, how they are liberated and dispersed and how their incidence varies from day to day and from place to place. The U.S.A. apart, there seems to be plenty of scope for such studies in most parts of the world, and workers in this field everywhere, especially those who are already familiar with Dr R. P. Wodehouse's earlier work on pollen morphology, will therefore welcome his latest handbook.

The author's opening chapter contains a summary of methods of sampling which though useful is not critical. Thus the oldest method, which also has been and probably still is the most widely used, is that of exposing horizontally a flat slide previously coated with an adhesive and kept sheltered from rain. It is very easy and convenient, but it is open to the objection that when the pollen rain is at all scanty the results obtained are imprecise, a fact which is made immediately apparent by analysing the pollen deposited on two equal areas of say 5 sq.cm. on one and the same slide, and has been further emphasized by an experimental investigation published in 1944 by Durham. It is only fair to add that this section of the book does not profess to be exhaustive.

Hayfever Plants, as its subtitle implies, is concerned in the main with the allergenic flora of North America. This subject is dealt with both taxonomically and geographically. In the systematic section are described not only all the plants known to cause hay fever in North America but also many others which are or have been only suspected of doing so. The author states that allergenic toxicity is limited to relatively few families, the fourteen most important of which he names at the outset, but he also describes sixteen more. Each family is briefly characterized with special reference to pollen productivity, its pollen grains are described, the most important species are referred to and their salient features and distribution are stated. For British readers interest will naturally centre on those groups in the British flora which are associated in America with hay fever and, of these, grasses are by far the most important. The author implies that sensitivity to one kind of grass pollen does not necessarily involve sensitivity to all, though this is debatable: one well-known English physician claims to have desensitized a patient who was allergic to pollens of native British grasses by treatment with an extract of sugar-cane pollen. It seems likely that the incidence of grass pollinosis is related closely to local concentration of grass pollen in general and its avoidance a matter of choosing areas where this concentration at the relevant times is negligible. Among British plants the next largest group inculpated is that of the catkin-bearing plants, in particular birches, oaks, elms and poplars, while other trees include the maple, walnut and ash. Pollens belonging to all of these genera have been caught, mostly in large quantities, at stations in Britain ranging from the south of England to the north of Scotland, and some of them may well cause hay fever in this country, but so far no proof of this has been brought forward. The same applies to the principal herbaceous types (other than grasses) concerned, viz. the plantains, chenopods and *Artemisia*. It is the more remarkable that the last-named genus has not so far been convicted in Britain when it is borne in mind that it is regarded by Dr Wodehouse as constituting, next to one other genus of Compositae (viz. *Ambrosia*) and possibly the grasses, the most important group of hay-fever plants occurring in America.

In the geographical section of the book the author presents a compilation of 135 regional surveys of hay-fever plants which have been published for various parts of the U.S.A. Wodehouse recognizes for this purpose ten regions, for each of which he gives an annotated calendar of hay-fever plants, showing week by week throughout the year those plants the pollens of which are likely to cause hay fever.

Dr Wodehouse has amassed and made easily available for the first time a wealth of information on the atmospheric pollens of North America. American allergists, for whom it is primarily intended, should therefore find it quite indispensable. But students of other branches of science than medicine, especially floral biology, plant breeding and quaternary geology, should also benefit, and it cannot be doubted that further fundamental studies on atmospheric pollen would be similarly fruitful.

H. A. HYDE

Recent Advances in the Chemistry and Biology of Sea Water. By H. W. Harvey, Sc.D., F.R.S. $5\frac{5}{16} \times 8\frac{1}{2}$ in. Pp. viii + 164. 29 text-figures. Cambridge University Press. 1945. 10*s*. 6*d*. net.

The sea is the chief intra-mundane regulator of atmospheric conditions and hence, in the long run, all living organisms, be they marine, fresh-water, or terrestrial, are affected by changes in the sea. At least a general understanding of these changes is therefore of very great value to every student of any biological problem which can be by any stretch of the meaning of the term considered to be an ecological one.

The sea is also *the* Pandora's box of surprises, and both for this reason—a reason which helps to keep the mind of the marine student particularly alert—and because the basic problems of cycles and of interchange between medium and organism are fundamentally alike in all ecological studies, a knowledge of, rather than a nodding acquaintance with, recent work on the chemistry and biology of sea water cannot fail to be of very great value to workers in many fields.

A very large number of people should be, for these reasons at least, very grateful to Dr Harvey for having undertaken the Herculean task of making available in a small space the results of the enormous amount of work which has been done during recent years in this particular field, work to which he has himself contributed to no small extent.

Chapter I, 'Introduction', deals especially with the various movements which enhance or restrain the mixing of waters from different regions.

Chapter II deals with '"Salinity", "Chlorinity" and Specific Gravity', and includes some details of modern methods of estimation.

Chapters III, IV and V discuss respectively 'The Major Constituents; The Minor Constituents; Dissolved Oxygen, etc.', the 'etc.' being mainly nitrogen.

Chapter IV indicates, *inter alia*, that very little work has been done on organic compounds.

Chapter VI, 'The Carbon Dioxide System', which describes methods in considerable detail, contains much that will appeal directly to those who are mathematically minded but cause others (as it did the reviewer) to do a lot of hard thinking.

'The Distribution and Estimation of Phosphate and of Salts containing Nitrogen' is the topic of Chapter VII, which again includes methods in some detail.

Chapter VIII, 'Changes due to Bacteria', is in many ways not only the most interesting but also the most important, if only because bacteria are not usually, even in the minds of biologists, thought of in connexion with the sea.

'Regeneration of Phosphate and Salts containing Nitrogen' and 'The Fertility of Ocean Water' are the subjects of Chapters IX and X. Perhaps the most significant point made in the latter is the importance of the 'physiological conditions' of members of the phytoplankton.

Each chapter is followed by an extensive Bibliography, while an Index of Authors and a Subject Index, both very full, make every part of the book readily accessible.

Regarded as a whole the book is well and lucidly written, while the text-figures—the majority of them graphs—are most helpful, which makes it a matter of especial regret that in several places the author confuses 'excreting' and 'voiding', talks of 'bacterial tissue', the 'grazing' of bacteria by the zooplankton—a sense in which the word 'grazing' is, unfortunately, being more and more used—and of flagellates and ciliates as 'invaginating' solid particles. Dr Harvey also follows the rapidly increasing number of writers who confuse 'more than' with 'as much (or as many) as', 'absence' with 'presence' in the phrase 'absent in', and use the words 'also' and 'either' without any regard to their positions in a sentence.

L. W. RENOUF

A Source Book of Agricultural Chemistry. By C. A. Browne. $10\frac{1}{4} \times 6\frac{3}{4}$ in. Pp. 290 + x with Frontispiece and 32 figs. in the text. Waltham, Mass.: Chronica Botanica Co.; London: Dawson and Sons. 1944. $5.

Dr Browne has Liebig for his hero. He begins his book with a frontispiece of Liebig's laboratory at Giessen, surely one of the most engaging drawings of a working laboratory ever published, and ends it with a concise record of Liebig's life and work. The intervening 270 pages are written to clarify the origins of agricultural chemistry and 'the relationships of Liebig's work to that of his predecessors'. The record is cut short at 1852, the date at which Liebig retired from Giessen to a period of relative sterility at Munich. It results that other pioneers of the mid-nineteenth century appear only as adversaries in Liebig's interminable polemics.

Dr Browne's admiration for Liebig is profound. He roundly calls him 'the central and most influential figure in the history of agricultural chemistry'; but he is not deceived, and he clearly states his hero's impulsiveness, his lack of discrimination in selecting data, his dogmatism and his bad temper in controversy. Through these clouds there break the bright gleams of his fertility of mind, his inspiration of a long list of distinguished pupils, his resource and enduring patience when a practical investigation had been undertaken, and his tenacity of the scientific principles he considered good. There emerges from this stormy picture an impression of power that may well be an object of admiration.

Liebig's training was that of an organic chemist and Dr Browne aptly remarks that this did not qualify him to be an authority on agricultural chemistry and, still less, one might add, on practical agriculture. From biological data he drew conclusions which may have been faulty in principle, but which were certainly vitiated by the circumstance that the biological 'facts' could not bear the weight of inference which he, as a chemist, expected them to. It has to be admitted that in this misfortune Liebig has had his successors, and it is perhaps one of the outstanding difficulties in the borderlands between sciences that data obtained on one side of the boundary appear so much more impressive when viewed from the other. Liebig himself evidently had some perception of this and is said to have complained that 'My endeavours to be of some use to physiology and agriculture are like rolling the stone of Sisyphus—it always falls back on my head and I sometimes despair of being able to make the ground firm'.

Dr Browne's admiration of Liebig does not cause him to be unfair to Liebig's coevals. He concludes his account of Boussingault's work by saying: 'Boussingault, Liebig and Mulder were close contemporaries, and each was the founder of an important school of agricultural chemical research. In general agricultural significance the work of Boussingault was by far the most important; his writings, because of their even calmness of tone and absence of personal antagonisms, were not so conducive to publicity as the more sensational contributions of Liebig. Boussingault, who lived to a serene old age, had the satisfaction of seeing the principles of his work adopted in all parts of the world.'

The scope of this book is very much wider than has been indicated so far, and it would be grossly unfair to the author to take his preface at its face value. He has, in fact, produced an account of agricultural chemistry from the time of the Greeks of the seventh century B.C. to the recent eighteen-fifties. Remarking, in an introduction, that there has never been much agreement upon the meaning and scope of the term 'agricultural chemistry', he has not allowed himself to be confined within any pedantic boundaries in following the work of the earlier investigators. There is, however, something rather out-of-scale in his statement that 'the atomic philosophy of Democritus...is the earliest expression of a comprehensive scientific theory of "*agricultural chemistry*"', and that the 'opposing system of Aristotle' hindered the efforts of the eighteenth and nineteenth centuries to found it.

The author's historical method is what he would himself call the biographical one; that is to say, he provides successive biographies of some fifty or sixty outstanding figures, describing the life and work of each in turn. Each biography is to a large extent an item complete in itself, even to having its own list of references. Nevertheless, a reasonable degree of continuity is achieved without any undue amount of repetition. For example, the 'Law of the Minimum' is dealt with in writing of Carl Sprengel, whom the author regards as its first announcer, and is not recapitulated in speaking of Liebig.

This is called a *Source Book* because the author allows his subjects to 'speak for themselves' through the medium of copious quotation. It is possible that the method has been carried rather far, since Dr Browne's own easy and economical style is likely to be more eloquent to a modern reader than a good deal of formal seventeenth- and eighteenth-century prose. In short, he shows that in his own generation he is better able to speak for them than they for themselves. His book is readable and interesting and likely to appeal to a wider circle of biological readers than those directly concerned with agricultural chemistry.

W. O. JAMES

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FACTORS INVOLVED IN THE REACTION BETWEEN PLANT CELLS AND SUBSTANCES AFFECTING GROWTH

THE PRODUCTION OF SWELLINGS ON ETIOLATED HYPOCOTYLS OF *HELIANTHUS ANNUUS* BY HETEROAUXIN

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(With Plate 1 and 3 figures in the text)

INTRODUCTION

Among the familiar reactions between heteroauxin and plant cells, that of causing swellings on stems or hypocotyls was early realized. Such swellings are the result of (*a*) the induction of meristic growth in cells or tissues which, generally speaking, would not normally develop in this manner, and/or (*b*) isodiametric expansion of cells of certain tissues which normally increase in size in an anisodiametric and polar manner.

The present study is concerned with the production of swellings in etiolated sunflower hypocotyls, the swelling, under the conditions of the experiments, being essentially the result of isodiametric increase in size of the cells concerned. The part played by roots and cotyledons in the swelling process are brought under discussion, and a suggestion is made as to the nature of the fundamental reaction between plant cells and heteroauxin.

The literature on the occurrence of such swellings is adequately covered by Czaja (1935), Went & Thimann (1937), Boysen Jensen (1936), Diehl, Gorter, Iterson & Kleinhoonte (1939), Heyn (1940) and Overbeek (1944), and need not be reviewed here.

METHODS AND MATERIALS

Seeds of Carter's *Helianthus annuus* var. Southern Cross were soaked overnight and the seed coat then removed to ensure better germination during the subsequent 24 hr. At the end of this period healthy germinated embryos were planted in glass tubes (approximately 8 × 2·75 cm.) filled with damped, sharp sand obtained locally and sufficient water added to wet the sand at the bottom. The seedlings were allowed to grow 2 days from planting and seedlings approximately 3 cm. high were used. On the third day a similar selection from later developing seedlings was also made.

The pastes employed had a basis of two parts lanolin to one part distilled water, together with the required concentration of heteroauxin or other substance under test. Unless otherwise stated the pastes were placed as a ring 0·8–1·0 cm. broad just beneath the point of attachment of the cotyledons, i.e. in the young developing cell zone.

All operations were carried out in the dark at 24–25° C., using a red light when required. The seedlings were always kept in an atmosphere of the maximum humidity obtained by means of a static layer of water on the bottom of the tanks containing the experimental series.

Each series consisted of ten seedlings, and within an experiment each series was adjusted to contain the same minor variations in length of seedlings. With the aid of a screw micrometer, diameter measurements were made at the beginning and end of the experimental period of 72 hr.

EXPERIMENTAL RESULTS

Relation between size of swelling and heteroauxin concentration

Serial dilutions were made with lanolin-water paste of a paste containing 10 mg. heteroauxin to 5 g. lanolin and 2·5 ml. distilled water, which concentration was designated Full Strength (FS).

Table 1. *Percentage increase in diameter of hypocotyls of* Helianthus annuus *with different concentrations of heteroauxin paste applied on young cell zone for 72 hr.*

Code concentration	mg. heteroauxin per g. lanolin-water paste	% increase in diameter
FS	1·330	8
FS/5	0·266	67
FS/25	0·053	46
FS/50	0·027	32
FS/100	0·013	24

As would be expected very dilute concentrations of heteroauxin had little or no effect on the diameter of the hypocotyls, but with increasing concentration progressively larger swellings were produced. Corresponding with the size of the swelling there was a simultaneous reduction in the normal increase in length, but even with such a concentration as FS/5 there was some increase in length of the area of application in the early part of the experiment. It is noteworthy, however, that at the FS concentration no swellings were produced in the young cell zone.

Relation between period of application and size of swelling

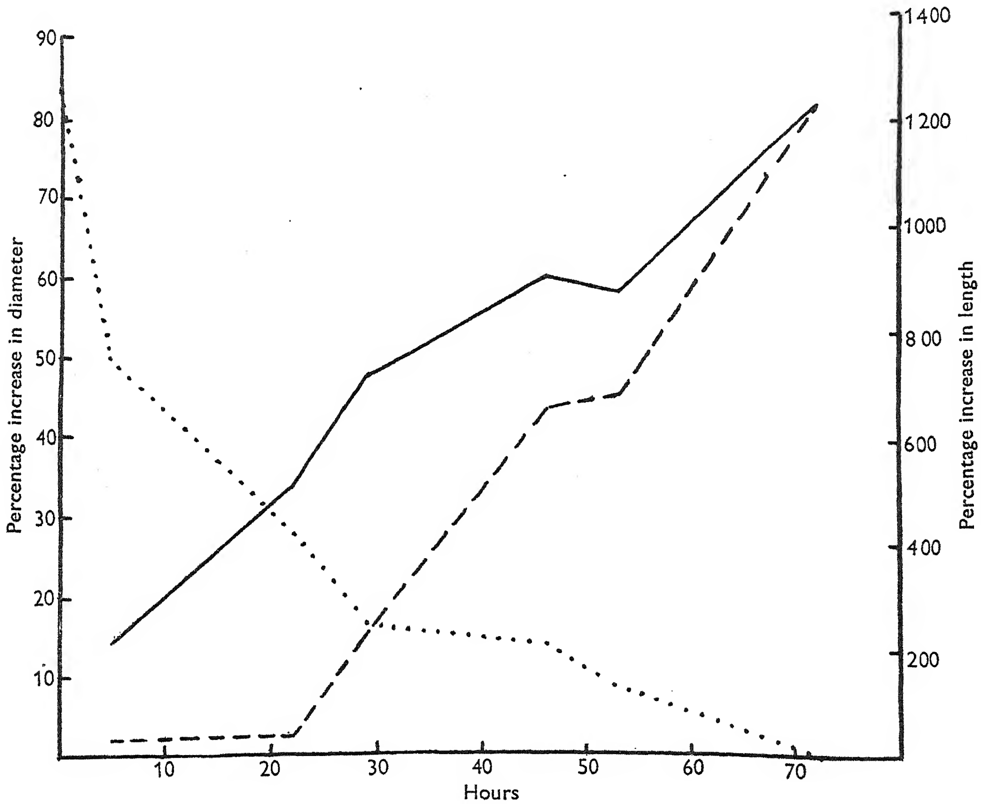
When heteroauxin paste is placed on the hypocotyl, lanolin and heteroauxin will start to diffuse into the tissues. The rate and degree of swelling will therefore depend on the rate of diffusion of heteroauxin into the tissues and on the time period required to induce swelling after an effective concentration of heteroauxin has arrived at the site of the reaction in the cells concerned. In the following experiment the rate of swelling over a 72 hr. period with FS/5 paste was determined together with the contribution of the various periods of application to the final 72 hr. swelling.

Six groups, of ten seedlings each, were selected and FS/5 paste applied as a ring in the young cell zone. The paste was removed from successive groups at 5, 22, 29, 46, 53 and 72 hr. and the diameters of the hypocotyls measured at these times. In this manner the rate of swelling was found. After these measurements, each successive group, now minus paste, was left to complete the 72 hr. experimental period and measured again in order that some measure of the contribution of each period of application to the final 72 hr. swelling could be obtained.

The results of this experiment, given graphically in Text-fig. 1, show that swelling did not commence to any significant degree until about 22 hr. or so from the commencement of the experiment, but that there was a subsequent increased rate of swelling which was maintained throughout the experimental period.

If, however, the final 72 hr. swellings resulting from each period of application are considered (unbroken line), it is found that an initial stimulus of only 5 hr. duration was sufficient to cause some degree of swelling and that successively longer initial periods of application proportionately added to the final 72 hr. swelling.

It would be apparent, therefore, that although there was no significant indication of swelling in the first 22 hr. of the experiment, sufficient heteroauxin had entered the tissues in the first 5 hr. at least to induce the process, but either had not reached the actual site of the reaction in effective concentration or, if it had, then there was a definite lag period



Text-fig. 1. Broken line: rate of swelling over 72 hr. period. Unbroken line: final 72 hr. swelling resulting from initial x hr. application of FS/5 paste. Dotted line: increase in length of marked area after removal of paste at x hr.

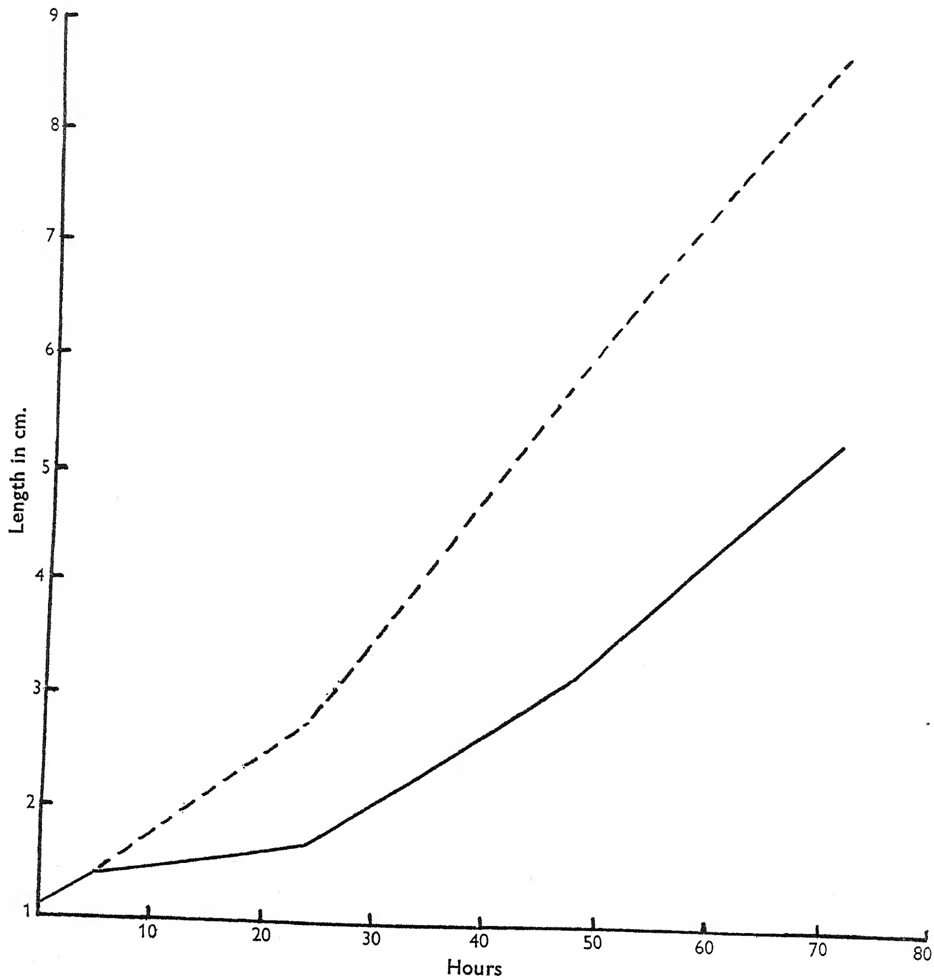
between the arrival of an effective concentration and measurable indication that swelling was occurring.

After removal of the paste at the various time periods it was observed that during the periods remaining until the end of the 72 hr. experimental period, growth in length could continue, or if this had ceased, showed signs of restarting in most instances. The dotted line (Text-fig. 1) indicates the percentage increases in length which occurred, during the terminal period $72-x$ hr., of equivalent short apical lengths of the hypocotyls marked *after* removal of the pastes at x hr.

In this respect it is apparent that such a short period of application as 5 hr. was

sufficient to cause a reduction in increase in length, a fact no doubt correlated in some degree with the production of small swellings as a result of such a period of stimulus.

This 5 hr. effect on length increase was examined in greater detail (Text-fig. 2), but it is to be remembered that the system of marking the required length of the hypocotyl was different in this experiment so that, while the 72 hr. relations between these measurements and those shown in Text-fig. 1 are similar, the absolute measurements must necessarily show a relative quantitative difference.



Text-fig. 2. Total length of marked region at hours indicated. Broken line: control group. Unbroken line: treated group.

In this experiment a length of approximately 1 cm. was marked off on the hypocotyls of two groups of forty-eight plants each. In the treated group the FS/5 paste was applied between the two marking points and removed after 5 hr., while the other control group remained untreated.

It is to be observed that during the first 5 hr. at least, the controls and treated groups showed equal increases in total length of the marked region but, at some point subsequent

to the removal of the paste at the 5 hr. time period but before the measurement at 24 hr., retardation of polar extension occurred in the treated group. Between the 24 and 48 hr. measurements the treated group resumed a higher rate of increase of total length of the marked region, and this was maintained during the rest of the experimental time period. Neither the total length nor rate of increase in total length of the marked region at any time became equal to the controls.

As regards *increments* in length of the marked region of the hypocotyl (Table 2) the treated group gave a value of about 0·6 cm. for the first 24 hr., rising to 1·5 cm. for the second and 2·1 for the third 24 hr. periods. The untreated controls showed increments of 1·7, 3·0 and 2·9 cm. for the successive 24 hr. periods.

Table 2. *Increments in length of marked region of hypocotyls of* Helianthus annuus *over three consecutive 24 hr. periods. Treated groups were given FS/5 heteroauxin paste in young cell zone for 5 hr.*

Hours	Increments in length (cm.)	
	Treated	Untreated
0–24	0·6	1·7
24–48	1·5	3·0
48–72	2·1	2·9

Table 3. *Effect of removal of roots on final 72 hr. percentage increase in diameter of hypocotyls of* Helianthus annuus *treated with FS/5 heteroauxin paste in the young cell zone*

Hours from commencement at which roots removed	% increase in diameter
0	25
17	37
24	39
72	62

Relation between roots and cotyledons and the swelling process

If the complete root system was removed at the commencement of the experiment when the FS/5 paste was applied in the young cell zone there was a marked reduction in the size of the final swellings though a small but definite increase in the diameter of the hypocotyl could be measured (Table 3). Such a complete removal of the roots after successive periods of time throughout the experimental period had progressively less effect on the final 72 hr. dimensions of the intumescences.

With such a removal of the roots, two of the possible effects on the plant would be (*a*) reduction in water intake together with the removal of the force of root pressure to assist water movement upwards, and (*b*) decrease in *active* absorption and accumulation of dissolved salts and their transference upwards. For if the roots are excised absorption of water and salts can only occur mainly through the relatively small area of the cut end; whereas when the roots are intact there is a large surface area for removal of water and salts from the external medium.

The experiments were done using washed gravel sand as bought locally and damped with tap water, but while there were some soluble salts present these would only be in relatively dilute solution. In order to elicit some information on the possible relation of

salts and water to the swelling process experiments of the type detailed in Table 4 were set up.

In this experiment the normal control in sand and adequate tap water was maintained and there was another control where the seedlings were merely removed from the sand and replanted in similar sand moistened with distilled water. In another experimental group the seedlings were replanted in sand damped with culture solution (KNO_3 0·25 g., $MgSO_4$, $7H_2O$ 0·125 g., Na_2SO_4 0·125 g., NaCl 0·125 g., KH_2PO_4 1·6 g., distilled water 1 l.). This group showed a significant increase over controls in regard to final swelling measurements. Much larger increases were found, however, where the plants were transferred to culture solution without sand, while transference to distilled water alone resulted in swellings similar or not quite so large as controls. In the last series in Table 4

Table 4. *Effect of addition of dissolved salts on the final 72 hr. percentage increase in diameter of hypocotyls of* Helianthus annuus *treated with FS/5 heteroauxin paste in the young cell zone*

Series	% increase in diameter
Control in sand, not changed	79
Transferred to sand damped with distilled water	76
Transferred to sand damped with culture solution	97*
Transferred to distilled water	66
Transferred to culture solution	135*
Transferred to culture solution, roots removed	47
Transferred to humid atmosphere, no sand or fluid	26

* Tendency to split in pith in some plants.

Table 5. *Effect of decapitation on final 72 hr. percentage increase in diameter of hypocotyls of* Helianthus annuus *treated with FS/5 paste in the young cell zone*

Hours from commencement at which hypocotyls decapitated	% increase in diameter
0	34
5	38
24	58
72	70

the plants were removed from the sand and merely left in a humid atmosphere in which case only slight swelling occurred.

It is to be noted that in those seedlings in culture solution alone, the swelling seemed to be so great that the tensions set up caused the hypocotyls to split at the pith. On occasion an intra-hypocotyl bifurcation could be obtained in the area of application of the paste. These effects made actual swelling measurements difficult to assess accurately, but nevertheless the production of increased swellings in the presence of the salts was self-evident.

Decapitation of the hypocotyls also resulted in a much smaller swelling, as reference to the experiment in Table 5 shows. There was, as in the minus roots experiments, a small but definite swelling when the decapitation occurred at the commencement of the experiment, while decapitation at successive intervals throughout the experimental period was reflected in the increasing dimensions of the final 72 hr. swelling, the undecapitated control being the largest.

If decapitation and removal of the roots were done simultaneously (Table 6) at the commencement of the experiment there was a more profound effect than if either was done alone, as in such cases no swelling occurred. As would be expected decapitation and removal of roots simultaneously and at successive intervals permitted the induction of successively larger 72 hr. swellings.

Table 6. *Effect of simultaneous decapitation and removal of roots on final 72 hr. percentage increase in diameter of hypocotyls of* Helianthus annuus *treated with FS/5 paste in young cell zone*

Hours from commencement at which excision done	% increase in diameter
0	4
24	38
48	52
72	64

Relation between stage of development of tissue and swelling

One method of considering the relations between age of tissues and the swelling process is to apply the heteroauxin paste at different levels of the hypocotyl, but in this type of experiment the size relations of the cells concerned have, as a result of normal polar increase in length, produced tissues, the cells of which may have reached the limit of extensibility.

In the following experiment (Table 7) various concentrations of paste were placed as a ring (*a*) in the young cell zone and (*b*) about 2 cm. lower down, i.e. near the base of the hypocotyl of the young seedlings.

Table 7. *Effect of heteroauxin concentration and of position of application of the paste on the percentage increase in diameter of hypocotyls of* Helianthus annuus

Code concentration	% increase in diameter Position of paste		
	Young cell zone	Base	
		Point of application	Above point of application
FS/5	46	7	16
FS/10	54	7	8
FS/20	53	3	4
FS/40	39	3	3

Most of the pastes caused a formation of swellings in the young cell zone, but in the older part none caused any (or only slight) swellings at the point of application of the pastes. Nevertheless, when applied in those lower zones, the heteroauxin obviously diffused up the hypocotyl and, with the relatively more concentrated pastes, caused swellings to form in the intermediate regions between the old and young cell zones, such swellings being smaller than the corresponding swellings in the young cell zone. A result with FS paste was obtained in an experiment some 19 months prior to the other data in the table. With this concentration there was no swelling in the young cell zone,

no swelling at the point of application of the paste, but definite swelling above the point of application.

As a further investigation on the effect of age of tissue on swelling some experiments were carried out (*a*) in which the complete root system was removed and the paste applied in the young cell zone at 0, 24 and 48 hr. from such removal. As the hypocotyl was constantly growing some of the components of the young cell zone were passing into the older cell zone so that the cells concerned in the swelling reaction at 48 hr. were not necessarily those which would have been involved at nought hours; (*b*) a similar control series with complete plants; and (*c*) a series where the hypocotyls were decapitated and the cells beneath the cut end allowed to mature before application of the paste at the times given for the other series. In this decapitated series, growth in length was small compared with the other series, so that the cells concerned in the reaction had extended in length some relatively smaller degree in relation to their possible maximum.

Table 8. *Percentage increase in diameter of hypocotyls of* Helianthus annuus *when decapitated or roots removed and plants left some hours before application of paste for a further 72 hr. period*

Hours before application of paste	% increase in diameter		
	Minus roots	Decapitated	Whole plants
0	53	45	78
24	47	11	65
48	31	2	47

With whole plants the young cell zone in this experiment showed an increase in diameter of 78% when the paste was applied immediately while in the 24 and 48 hr. series the increases were 65 and 47% respectively. A similar trend occurred in the series without roots, the swellings in 0, 24 and 48 hr. series being 53, 47 and 31%. In the decapitated series, however, the cells definitely lost the capacity to react to the hetero-auxin, this being almost completely so in the 24 hr. series.

In order to maintain the young cell zone over relatively long periods with no change in cellular constitution or degree of elongation, seedlings were kept in the dark in a domestic refrigerator at about 1–3° C. for different periods of time, with subsequent transference to 25° C. and application of paste for the usual 72 hr. period. While no precautions were taken to guard against variation of the cold temperature, temperature gradients were overcome by staggering the individuals of each series in equivalent positions. There was an occasional loss of a few seedlings by death through cold.

A point of importance in this experiment is that the young cells can be maintained in the same stage of development for at least 3 days from the actual commencement of the experiment and yet retain much the same potentiality to produce swellings. The increases in length of the marked zone are also of interest, as there is certainly no decrease in rate of increase from the time of retransference from the cold temperature to 25° C. as compared with the control untreated series. Indeed, there is evidence that the period of refrigeration caused an augmented rate of increase in length, and the extension between the marks 3 days after transference to the warm temperature was greater than the 3-day measurements of the untreated controls. It was observed that the retardation of growth

in length between the marks as a result of a 3-day application of FS/5 paste was not permanent and extension could be resumed after removal of the paste (Table 9).

Table 9. *The effect of refrigeration on increase in length and swelling capacity of hypocotyls of* Helianthus annuus

Treatment before transfer to 25° C.	Average length of marked zone (mm.)								% increase in diameter 3 days after application of FS/5 paste
	Days from transfer to 25° C.								
	0		1	2	3	4	5	6	
1. None. No paste	—	1·0	1·65	3·26	3·9	4·4	—	4·5	—
2. 24 hr. in cold. No paste	(1·01)*	1·05	2·3	3·6	4·4	—	4·9	—	—
3. 72 hr. in cold. No paste	(1·03)	1·13	2·5	—	5·2	—	—	—	—
4. None. FS/5 paste	—	1·03	1·45	1·77	2·2 Paste removed	2·7	—	3·4	48
5. 24 hr. in cold. FS/5 paste	(1·03)	1·03	1·5	1·8	2·2 Paste removed	—	2·9	—	58
6. 72 hr. in cold. FS/5 paste	(1·01)	1·1	1·11	—	2·2	—	—	—	39

* Figures in brackets represent original length in mm. of marked zone before cold treatment.

Discussion

It is apparent from the results of these experiments that, in the type of heteroauxin-induced swellings studied, the roots (Went, 1938) and cotyledons play an important part in the swelling process. For the induction of maximal swellings both organs must be present throughout most of the swelling period, and if either or both are removed, a definite reduction in the size of the 72 hr. swelling is found (Tables 3, 5 and 6).

While swelling can proceed to a limited extent in the absence of either of these organs, the effect is more profound in the simultaneous absence of both from the commencement of the experiment, in which case no swelling occurs. The factors from both organs apparently have an additive effect in the production of such swellings.

One of the functions of the root and cotyledon factors probably lies in the maintenance of the osmotic relations of the swelling cells. It is certain that so far as the roots are concerned the degree of swelling can be considerably increased by the addition of dissolved salts to the external medium.

Another root factor would, of course, be water, an obvious necessity in the swelling process. In the absence of roots water can only pass into the hypocotyl mainly through the cut end and the force of root pressure, normally facilitating the upward movement of water and dissolved salts, would be absent. Water is not to any extent withdrawn from other tissues as the last series in Table 4 shows. Here the plants on removal from the sand and transference at the beginning of the experiment to a humid atmosphere, remained turgid and fresh but only small swellings were formed.

In the distilled water series in Table 4 the swellings approach those of the control sand series, and this might lead one to suppose that water is one of the main factors coming from the root. However, we are as yet unaware to what extent: (1) accumulation of salts in the roots occurs before the experiment commences, (2) translocation of these to the site of the reaction occurs, or (3) the degree to which electrolyte from the glassware dissolves in the water.

With regard to the cotyledons it might logically be considered that these also could supply osmotically active substances, e.g. sugars. Preliminary work has indicated that the presence of sugar in the paste in some measure replaces the excised cotyledons, but the experiments were not sufficiently controlled for reporting in this paper. It has, however, been observed by others (Bausor, 1942) that sugars can replace the leaves in regard to the formation of intumescences in the bean, where, in contrast to the present series, cell division was the primary cause of increase in diameter.

There is, however, another relation between the cotyledons and the swelling process, viz. the effect on ageing cells. If the hypocotyls are decapitated they seem to lose the capacity to swell to any extent if left for 24 hr. under the working conditions before application of the paste (Table 8). A tendency in this direction might be expected as the cells extend in length during this pre-experimental period. But they do not do so to their potential maximal lengths, so that swelling, though to a lesser extent, should still be possible. It would seem, therefore, that the cotyledons play a part in the normal extension in length of the hypocotyl and in the maintenance of the capacity of the cells to swell isodiametrically. In addition to possible osmotic effects there has been a hitherto inadequately explained relationship between heteroauxin and sugars, and if the effect of the cotyledons in the present experiments proves to be mainly a sugar factor the result would emphasize the necessity of further exploratory work on the details of this relationship.

In Table 8 it is also seen that the degree of swelling in complete control plants decreases with age, and if the seedlings are left 48 hr. after the normal time for commencement of the experiment, the 72 hr. swelling in the young cell zone is 147 % of the original diameter as compared with 178 % in the nought hour control series. A similar trend is evident in the minus root series, a result to be expected in view of the results with the complete control plants, but the absolute values are less in accordance with the findings in the minus root series in Table 3.

The possibilities here are: (1) the total number of cells in the young cell zones are decreasing in number and thus accounting for decreased swellings, or (2) there is a gradual diminution or exhaustion of a cotyledon factor active in the swelling process.

Thus, to inhibit or retard swelling, the reacting cells can be denied factors from the root and cotyledon or they may be allowed to extend anisodiametrically so that they reach a stage at which they become unreactive in respect to swelling.

It is possible by cold treatment to dissociate the effect of mere age of cells from that of the root and cotyledon factors but with the limitation that cold treatment would also retard that series of reactions collectively causing the so-called 'ageing' of cells. If the seedlings are maintained at a low temperature over a period of 72 hr. at least (Table 9), the young cell zone still has the capacity of producing a degree of swelling, during a further period of 72 hr. with FS/5 paste, approaching that obtained without preliminary cold treatment. The mere fact of age, therefore, within the limits of the experiment given, is not critical in relation to a reduction of the capacity to swell but rather the processes which lead to 'ageing'.

It is possible that many questions raised in the preceding discussion would be answered after further experimentation. More difficult to solve, however, is the problem of the effect of the heteroauxin itself.

In the present study only one expression of the reaction between cell contents and heteroauxin has been considered. There are many other familiar expressions of the

reaction between cell and heteroauxin, and of these we need only mention stimulation to cell division, prevention of leaf fall, fruit setting and so on. The question which confronts the biologist is whether this substance (together with all other such growth substances showing these various effects in differing degree) has a multiplicity of reactions corresponding to the multiplicity of effects or if, in fact, there is some basic, fundamental reaction which finds expression in different ways according to the nature of the cells concerned. The present author considers the latter view to be the more reasonable, but with this, two important questions become outstanding: (1) the relationship between the various growth substances and (2) their mode of action.

In regard to (1), much thought has been devoted to this question of the relationship of the auxins, especially that based on chemical structure (Kögl & Kostermans, 1935; Koepfli, Thimann & Went, 1938), but here it may be that attention should now focus, not on such a relationship to one another, but rather on their relationships to a substance or group of substances of a higher order of complexity within the cell.

However, our lack of knowledge on the actual fate of the auxins is still profound, and one might with equal force suggest that these growth substances or a resultant compound form a complex (prosthetic group) with protein or enzyme (Skoog, Schneider & Malan, 1942).

Similarly, the mode of action of the auxins (direct or indirect) has not been explained by experimentation, and it seems to the author that to solve this vital problem we must have more specific knowledge of the cell at what is the ultramicroscopic or even the molecular level.

So far as one constituent of the cell is concerned, namely, the cell wall, we have been given some indication of its ultramicroscopic characteristics. It is, in effect, a three-dimensional lattice, the units of which are fibrils of cellulose molecules or in part simple chains of these (Frey-Wyssling, 1939). That author suggested that one of the effects of heteroauxin is to loosen the heteropolar points of attachment in the cell-wall lattice, thus increasing its plasticity (Heyn, 1940).

This theory lends itself to attempts to explain the polar increase in cells and the maintenance of 'Rohrenstruktur' (Frey-Wyssling, 1939; Diehl *et al.* 1939; Borgström, 1942), though it cannot sufficiently account for the differential sensitivity of the various cell walls of the same cell. In view of the fact that there are so many other effects induced by the auxins, it seems more likely that the fundamental reaction of relatively greatest importance involves some part of the protoplasm, a point of view suggested also by Strugger (1934) and others.

When the theories of the ultramicroscopic nature of the cytoplasm are considered, those of Seifriz (1923–4) and others that the cytoplasm is also a three-dimensional lattice composed of long molecules seems to fit most of the known chemical and physical properties of cytoplasm (Bensley, 1943). Inevitably, also, specialists in this field have concluded that there is some form of organization of the cytoplasm, and an analysis of this concept is discussed in Needham (1942). The term cytoskeleton (or 'cell skeleton') has been given to this system of organized molecules which would be arranged as a three-dimensional lattice; and if we admit the possible existence of the cytoskeleton it is natural to think of it in terms of a framework of protein molecules or fibrils upon which prosthetic groups, desmoenzymes, lipids, sterols, etc., could be attached.

In contrast to the cell-wall framework of cellulose, the cytoskeleton could not be

considered as relatively fixed but rather as a dynamic structure (Needham, 1942), in which the molecules or fibrils could disengage and reorientate in the same or different configurations. The system would, of necessity, possess the property of undergoing sol$\rightleftharpoons$gel changes according to conditions. The analogy between such a concept and the characteristics of thixotropy, where even mechanical shaking can change the system from the gel to the sol state, is real, but, as has been pointed out by others, with a relatively higher degree of complexity in the cytoplasm as one would expect.

From the viewpoint of the organization of a cytoskeleton it would suggest itself that the orientation, kind and relative frequency of the various molecules within the fibrils, or the orientation of the fibrils themselves, could have a formative influence on the various manifestations of cell behaviour, e.g. physiology, maturation, differentiation and processes leading to cell division.

It is, in fact, on such manifestations of cell behaviour that growth substances exert their influence, and in an attempt to rationalize such diverse effects the author has suggested (Jones, 1944), as an outcome of the above considerations, a working hypothesis which may be formulated thus: growth substances (auxins), by direct or indirect means, act upon the cytoplasmic lattice or cytoskeleton, by loosening or preventing the engagement of some bonds of attachment within or between certain protein molecules. These components of cell structure may then be in a position to reorientate in the same or a different configuration, and it becomes possible, in a tentative manner, to visualize how one can integrate the various effects of auxins. Cells which had become to all intents morphologically stable would once more be changed into a condition of instability with new potentialities and competences. Tissues such as the epidermis seem to be least liable to change, while others such as cortex, pericycle and phloem parenchyma (Scott, 1938–9; Borthwick, Hamner & Parker, 1936–7) are less fixed in this respect, and because of this can be caused to initiate meristems which are capable of producing morphologically different tissues (e.g. roots from cuttings).

In the same way reorientation of the components of cell structure could bring new molecular surfaces into contact with new or pre-existing substrates. Therein may be the explanation of the fact that some physiological or enzymatic processes are initiated or augmented by means of auxins in *in vivo* experiments (Commoner & Thimann, 1941), which processes are unaffected *in vitro* (Berger & Avery, 1943).

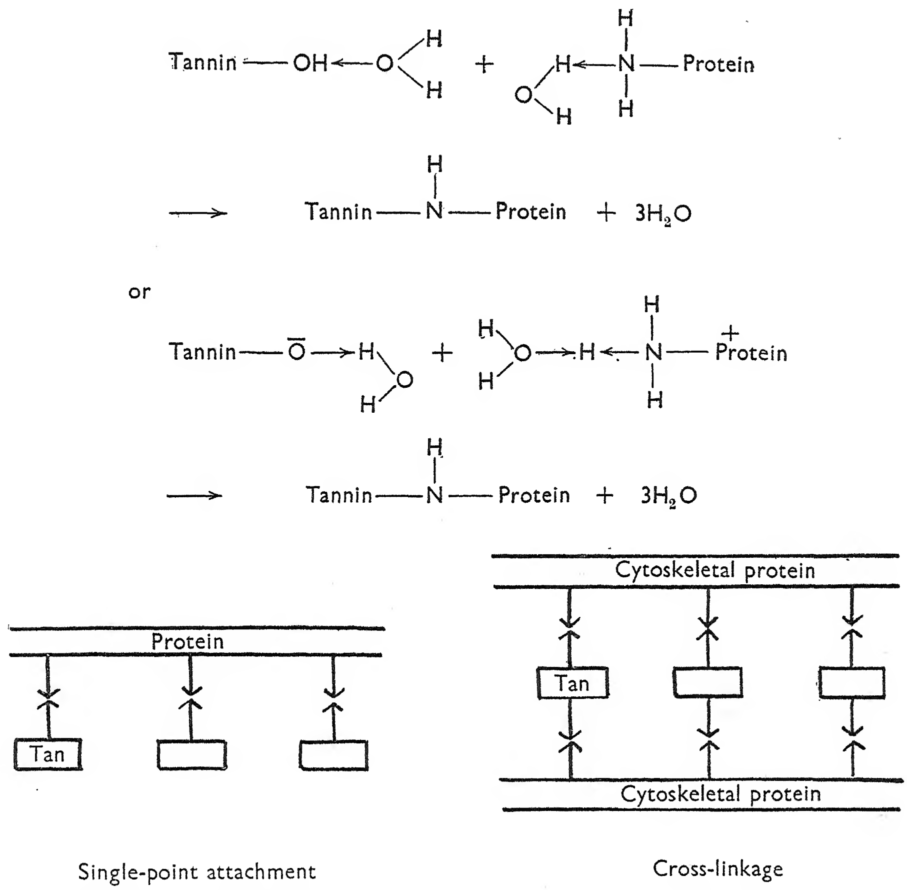
After publication of this hypothesis in the briefest terms (Jones, 1944) the present author found a paper by Northern (1942), which author suggested, on the basis of his protoplasmic viscosity studies, that auxins might cause a breakage of protein molecules of the protoplasm into molecules one-eighth or one-quarter their original length.

It is admittedly difficult to study the hypothetical three-dimensional lattices of the cell structure. As a contribution to this line of thought it was considered desirable to test a number of substances which have the potentiality of reacting with proteins. The molecules of some of these, by virtue of their stereochemical properties, could only attach themselves theoretically to single points on a protein molecule, but others, such as para-compounds, could, as suggested by Powell (1944), form cross-linkages between protein molecules or fibrils. Some insight into a possible reaction can be obtained from the theory of tanning by Lloyd (1934, 1935), and use is freely made of this in Text-fig. 3 to show how cross-linkage could be formed.

Such artificial cross-linkages should result in a more fixed cytoskeleton with possible

prevention of the hypothetical loosening of points of attachment by auxins. On a similar basis there remains the possibility of using substantive dyes which attach themselves to cellulose without the intermediary of toxic mordants and so prevent expansion of cell walls.

A number of these possible protein reactants were tried (*a*) using hypocotyls as in the foregoing experiments and (*b*) on roots where the natural auxin concentration in the tissues would be at a low level. In keeping with the already known differences which



Text-fig. 3. A method of single-point tanning of a protein molecule (Lloyd, 1935), and from this a possible method of forming cross-linkages between cytoskeletal proteins.

exist between roots and shoots it was found in general that the roots showed greater susceptibility to them than did the shoots. The experiments with roots will be reported in another paper.

With the shoots it was found to be more difficult to obtain quantitatively similar results. In general terms, however, it may be said that, in conjunction with FS/5 hetero-auxin-lanolin paste, catechol could inhibit the normal production of swellings, the epidermis, at a concentration of 2·5 mg./g. of paste, staining black while the underlying tissues were much lighter in colour and apparently healthy. Hydroquinone was less

active than the *ortho*-compound. Phenanthrenequinone was also inhibitory to swelling, while anthraquinone was not.

It is to be noted that in all cases with the substances mentioned and the phenylenediamines the usual inhibition in length due to the heteroauxin was always found. There is also evidence that these substances were able to move more freely into the tissues in the presence of heteroauxin.

Amino groups also have the potentiality of reacting with proteins, and it was found that in equivalent concentration *ortho*phenylenediamine was more inhibitory to swelling formation than the *meta*- and *para*-compounds. That these substances do enter the tissues and are translocated can be observed visually, for in the case of *p*-phenylenediamine, for instance, the cotyledons assumed a greenish blue hue while with *ortho*-phenylenediamine a definite orange coloration was formed. As regards this latter at least, it is an interesting fact that it passes up the hypocotyl and into the cotyledons (through the vascular system as freehand sections show) and out to the epidermis where it accumulates as orange droplets (Pl. 1).

There is thus striking evidence that the vital activity of all the tissues concerned is not impaired by these compounds.

Some anthraquinone derivatives produced results of an interesting nature. While a number of these derivatives, such as alizarin, purpurin, quinalizarin and some mono- and disulphonic acids were without any great effect in the concentrations used, it was found that the sodium salts of 1:2- and 1:4-dihydroxyanthraquinone sulphonic acids had the property of nullifying to a significant degree the effect of the heteroauxin paste. In other words, in the presence of alizarin red or quinizarin sulphonic acid (sodium salt), the 1:2 and 1:4 compounds respectively, a certain concentration of heteroauxin behaved as a weaker concentration of the auxin. The quinizarin compound was the more active in this respect.

There are at least two explanations of this phenomenon:

(1) A reasonable explanation is that the substances *or contained impurities* had destroyed some of the heteroauxin to the extent of reducing, for instance, a full-strength concentration to an approximate FS/5 or less concentration.

Such destruction could be by oxidation of the heteroauxin involving a possible reduction of the substance or impurity. However, the presence of reducing agents in the paste, such as dihydroxymaleic acid or ascorbic acid, did not affect the general result (Table 10).

Table 10. *The effect of the sodium salt of 1:4-dihydroxyanthraquinone sulphonic acid (Q) and of dihydroxymaleic acid* (D.M.A.) *on the percentage increase in diameter of hypocotyls of* Helianthus annuus *treated with heteroauxin-lanolin-water paste*

Composition of paste	% increase in diameter
FS/5 heteroauxin	83
ditto + Q (4 mg./g. paste)	12*
ditto + ditto + D.M.A. (10 mg./g. paste)	10*
ditto + D.M.A. (10 mg./g. paste)	77

* Corresponding large increase in length.

Similarly, aqueous solutions of heteroauxin with alizarin red had no greater instability than heteroauxin solutions alone and any losses which occurred, as measured photo-

metrically using the nitrite technique or by biological testing on root growth, were substantially the same in both solutions. In addition, keeping tests showed that a full-strength concentration of heteroauxin paste containing ten times the usual concentration of alizarin red (usual concentration 4 mg./g.) was still able to produce swellings after more than a week.

(2) The possibility still remains that these two substances, or impurities which they contain, are acting as substances forming cross-linkages in a very selective manner (Jones, 1944). Brain (1946), working with other anthraquinone derivatives supplied by these laboratories, briefly indicates agreement with this possibility, though she is apparently unaware of the previous published work on plant material using these anthraquinone derivatives.

Summary

1. Decapitation or the removal of the roots of the hypocotyls of seedlings of *Helianthus annuus* result in a reduction of swellings caused by heteroauxin paste.

2. It is suggested that the main contribution of the roots to the swelling process is the maintenance of water and dissolved salts. That of the cotyledons is possibly sugar, but there is another as yet obscure effect related to the ageing of the cells in the swelling region.

3. Exposure of the seedlings to cold temperature for at least 72 hr. does not substantially alter the final size of the swelling.

4. A possible mode of action of growth substances on plant cells is discussed, and it is suggested that such substances act on the cytoskeleton of cells.

5. Substances capable of reacting with proteins have been used with a view to tanning the proteins of the cytoskeleton. Many of these substances prevent the production of swellings by heteroauxin.

The work described in this account was done when the author was employed at Hosa Research Laboratories. Thanks are due to Miss Clifton and Mr Davey for valuable technical assistance. The author also wishes to acknowledge the permission given by Mr J. H. Thompson, Director of Research, to investigate the problem as a contribution to studies in abnormal growth and to publish this account.

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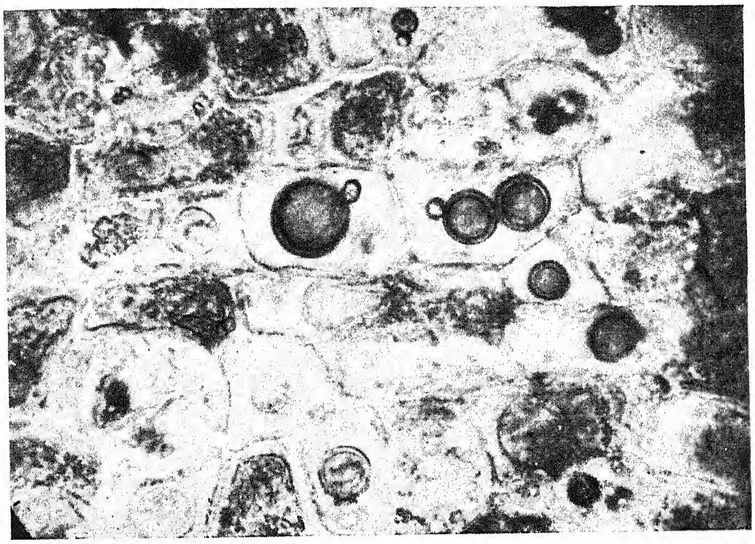


Epidermal peel taken from cotyledons of plants which had a heteroauxin-*ortho*phenylenediamine paste on the hypocotyl. Dark globules in cells are orange-coloured accumulations of the substance under test.

JONES—FACTORS INVOLVED IN THE REACTION BETWEEN PLANT CELLS AND SUBSTANCES AFFECTING GROWTH

SUGGESTIONS FOR BOTANICAL PROGRESS

By E. J. H. CORNER

Botanic Gardens, Singapore

Lack of knowledge of tropical flowering plants—unparalleled destruction—urgent need for nature-reserves—unsuitable 'floras'—headquarters of botany in the tropics—a botanical encyclopedia—advice to young botanists.

When I went to Malaya as a mycologist, I had the impression that the study of flowering plants was well advanced and that by chance observation there was little to be added. I confined myself to the fungi. But who can specialize amid such vegetation? The very trees inspire. I met in the forest so many beautiful fruits, such a variety of hooks and grapnels, barks and breathing roots, such curious forms of growth, immense leaves and ecological absurdities, of which I had never read in general botany, that I was driven to the flowering plants. I looked in 'floras' and in the herbarium, but neither in the books did I find mention of them nor in the herbarium specimens wherewith to identify them. Slowly, very slowly, there dawned on me the full meaning of the '*hortus siccus*'. These glorious objects, abounding, were known for the most part from dried specimens, described by persons in distant lands who had never seen the brilliance of the tropics, far less had felt their grand vivacity. Floras had been compiled from scraps of huge plants which could be fitted into cabinets and they had been collected mostly on hasty expeditions from such as were accessible and flowered commonly; while glimpses of the living had been afforded by precocious specimens in hot-houses. Could this be science that described a tree from one dried twig or sought to study palms on paper? What could we know of Gymnosperms, for instance, from such material?

For this unhappy state many explanations can be given, but none is suitable in the modern world. In temperate countries, which lead botany, systematists of tropical floras still guard their 'corroding' types, base species on single specimens, boil up solitary flowers and puzzle over blackened lumps, like mouldered oranges, to monograph families from a few bundles of such material, while in the tropics hundreds of thousands of these self-same plants are being burnt. In the last twenty or thirty years more primeval forest must have been destroyed botanically—cut over, extracted, alienated, improved, converted, to use departmental terms—than in any other generation and, botanically, with what advantage? What herbarium has used this unprecedented opportunity of falling trees to gather material of the inaccessible forest giants, lianes, palms, pandans and epiphytes?* And here lurks the fear which haunts me and which has made me change the microscope for the telescope, the razor for the axe, the trowel for the monkey, and to cast my eyes up, instead of down. I fear lest all the virgin lowland forest of the tropics may be destroyed before botany awakes: even our children may never see the objects of

* Requests for freshly preserved material from the Singapore Botanic Gardens have been extraordinarily few, mainly from cytologists. Dr E. D. Merrill, with his experience in the Philippines, organized one such collecting trip in Malaya on behalf of the Gray Herbarium, Harvard University. Yet the very common epiphytic pandan of Malaya seems never to have been named.

our delight which we have not cared for in their vanishing.* He needs hear but once the axing and the crashing in the glades, the silencing of birds and monkeys, and the crackle of the flames to know that Artemis has fled where Plutus starts to reign. Yet, so cheap is the earth's green mantle that, at the cost of a director's holiday, a botanical institution could intervene and enrich its meagre slips a hundred fold.†

I saw this devastation soon after I went to Singapore. It was the passing of the last big area of swamp-forest on the island, and I have always regretted my ignorance for it is the rarest forest to persist and the strangest and the least known. Yet, what occurred is nought to the thousands of acres which have disappeared on the mainland through alienation or conversion into so-called forest-reserves which, botanically, are but the stock-in-trade of a few timbers: and much of this destruction is wanton through careless or corrupt control, without provision for the future.‡ As an official in a tropical botanic garden, I saw that it was my duty to study the living trees and other large plants most in danger of destruction or before they were relegated to distant gullies, and to try to maintain true reserves of the original forest both near the large towns and in the foresters' reserves beside their 'improvements': it was a duty, also, to educate the people of the country to care for this heritage. In a few years, I turned from academic mycology to an urgent necessity and, in 1932, began the *Wayside Trees of Malaya* as an introduction to the country-life. It took eight years to complete. The long delay in a work so elementary arose from an obstacle which is the next problem. I found that existing botanical work was largely unsuited to my purpose and that I had to study every tree myself (over 900 common species||) in order to write correct descriptions. This failure of systematic botany is little realized but, as it must be universal in the tropics and will present itself to others, I will explain the chief difficulties.

1. *Ignorance of vegetative characters.* Trees and other large inaccessible plants, as palms, pandans, climbers and so on, are recognized firstly from their shape, general colour and bark: then from fallen leaves, fruits and seedlings: lastly from the flowers which, being the most fugitive parts, are the least seen. Systematic botany inverts the procedure, requiring flowers and fruits before leaves, and seldom mentions the primary points unless for a few well-known timber-trees. So, on most days of the year, when not in flower, these dominant plants cannot be identified.¶ It is becoming fashionable, too, to split genera and families, as well as species, and thus to make impossible their recognition

* Witness Java with almost no lowland forest, and Borneo with enormous areas of depauperate secondary forest reaching far up the mountains. As for Singapore, except for Bukit Timah Forest (150 acres) and a few parts of the Reservoir Jungle, there is no original forest within 40 miles (Gunong Pulai Water Catchment Area in Johore): it has gone within the living memory of the first Director of the Botanic Gardens.

† $3, or 7/6, an acre as Temporary Occupation Licence in Malaya, with rights to fell and burn all timber in virgin forest (1930–1940).

‡ Most hill-land in Malaya is 'barren' after a few years of pineapples. In a twinkling, the rich humus of millennia is washed off; and we continue to speak of agricultural science. What fine sanctuaries for wild life would be those ugly hill-tops in Johore!

|| And nearly all enter into the life of the Malayan countryman.

¶ Some trees do not flower more than once in 3–4 years, even longer, as is well known in palms (*Corypha, Caryota*) and bamboos. *Homalium grandiflorum*, a common Samydaceous tree in Malaya, flowers but once in periods of more than 10 years. A wild mango in Singapore fruited in 1929 but has not flowered since (Nov. 1945). I collected fruits of a *Coelostegia* (Bombacaceae) in 1930, but never flowers until 1940. Unless a botanist spends more than 12 months in Malaya, he may never collect material to identify its most characteristic trees, the Dipterocarpaceae. He will have equal difficulty in attaching flowers and fruits to the huge leaves of *Amorphophallus*. *Rotans* he will avoid.

'in the field', e.g. Caesalpinioideae and Mimosoideae, as splits from Leguminosae, and the new genera of *Quercus*. But why systematic botany should have made no effort to provide useful keys for the identification of the dominant plants of the tropical forests, as this must be the purpose of 'floras', I cannot understand except as the detachment of theory, at the desk in the *hortus siccus*, from the facts of nature.* It seems that keys which are not based on floral structure are deemed artificial and, therefore, unbecoming to a learned work. This view, I contend, is thoroughly mistaken and rather the academic lingering of the Linnean system, based on herbs, than scientific procedure. We know very well that vegetative characters are criteria not merely of species and genera, but of families, classes and phyla, as are the leaves of mosses, ferns, gymnosperms, Monocotyledons. And experience in the forest soon enables one from the features of bark, bole, branching and foliage to distinguish many genera and families of flowering plants. Unfortunately, systematists served with dried specimens have seldom been faced with the real problems of identification of plants in the tropics and in their learned detachment have elaborated the floral classification which may be more artificial than that based on vegetative characters. Thus, it happens that nearly every tropical flora is fundamentally unsuited to its subject, inasmuch as it is practically impossible to identify from them more than one tree in every thousand which are met with in the forest: they not merely discourage the aspirant by so aggravating his difficulties but they expose their authors to unlearned ridicule.† As a principle in a tropical flora, floral characters should never be used in keys and those of fruits only when they are obvious. If all the species of trees in Malaya (some 3000) were ranged together, there would, with few exceptions, be no difficulty in seeing their differences in vegetative character: likewise with palms, epiphytes, climbers and bushes. A book on tropical trees, to be successful, must be based on field knowledge.‡

Note. The importance of vegetative characters, so universally overlooked, must be illustrated in detail. That there is no *a priori* reason why the structure of flowers should be more fundamental than that of other parts of the plant is shown by the following facts.

(*a*) These families (to mention the better known) are at once distinguished from vegetative characters: Coniferae, Cycadaceae, Casuarinaceae, Palmae, Pandanaceae, Araceae, Gramineae, (? Cyperaceae), Musaceae, Marantaceae, Zingiberaceae, Orchidaceae, Dioscoriaceae, Dilleniaceae, Magnoliaceae, Menispermaceae, Annonaceae, Myristicaceae, Guttiferae (in Malaya), Dipterocarpaceae, Ilicaceae, Rhizophoraceae, Leguminosae, (? Rutaceae), Begoniaceae, Podostemaceae, Cactaceae, Ampelidaceae, Cucurbitaceae, (? Passifloraceae), Umbelliferae, Araliaceae, Rubiaceae, Ebenaceae, Sapotaceae (in Malaya), (? Bignoniaceae).

Probably few botanists have dissected the flowers of *Casuarina* or *Quercus* in order to identify them, thereby showing how *artificial* and academic are the 'keys' of systematic botany.

* Foresters, of course, realize this and the few botanical works which their botanists produce are more useful than the customary 'floras', e.g. Endert's *Geslachtstabellen voor Ned. Indische Boomsoorten naar vegetatieve kenmerken*. (Med. Proefst. Boschwez. no. 20, 1928), and Symington's *Foresters' Manual of Dipterocarps* (Malayan For. Rec. no. 16, 1943). These books mark a new era of real biology in tropical systematy— the study of the living, not the dead.

† To identify the unmistakable and now tropically universal *Delonix regia* (Flame of the Forest), the novice must, according to the floras, examine the aestivation of the petals. *Bougainvillea* needs far more detail, yet the anomalies of Hibiscus are seldom allowed for. An orchid is distinguished from a palm on ovary-structure. To separate the Oil palm (*Elaeis*) from the Coconut, according to the recent flora of West Tropical Africa (1936), one must examine the male flowers, yet a Malay child can do it by seeing, unwittingly, vegetative characters of equal generic value: it is, in fact, a more-than-generic feature that the trunk of the coconut palm can be notched for climbing, whereas that of the unclimbable oil-palm cannot.

‡ It would be well if a student of Angiosperms, on coming to the tropical forest, set about identifying trees from their roots. I have used this method successfully in the swampy peat-forests.

(*b*) In Malaya, many other families (Burseraceae, Meliaceae, Sapindaceae, Sterculiaceae, Moraceae) can be so identified and many genera (*Garcinia, Calophyllum, Cratoxylon, Ouratea, Antidesma, Baccaurea, Phyllanthus* sensu lato, *Aquilaria, Mangifera, Dialium, Dipterocarpus, Horsfieldia, Quercus* sensu lato, *Alstonia, Dyera, Terminalia, Elaeocarpus*). Any day, therefore, the species can be identified from trunk and fallen leaf. The bark is the only means of distinguishing *Ficus*-trees from *Artocarpus*, when sterile.

(*c*) In contrast, the flower-fruit system gives no comprehensive character for many big families, e.g. Leguminosae, Euphorbiaceae, Meliaceae, Sapindaceae, Rubiaceae, Sterculiaceae, Guttiferae, and Moraceae. In nearly every case the vegetative character is as reliable as the reproductive and, generally, less varied, e.g. Burseraceae and pinnate-leafed Anacardiaceae for which Engler relies on the ovule.*

(*d*) The reproductive system has led to the unnatural assemblages Polypetalae, Sympetalae, Apetalae, Archichlamydeae, Metachlamydeae, Parietales, Geraniales and so on. Several Mimosoid genera have sympetalous flowers with a corolla-tube as elegant as the Compositae, so that it is impossible to identify them in the current systems or 'natural keys'. Contrariwise, many Sympetalae are practically polypetalous (Myrsinaceae, Oleaceae, Ericaceae). The Ilicaceae and Cyrilleae have almost exactly similar, deeply partite, or narrowly sympetalous, corollas, but the Ilicaceae are Polypetalae and the Cyrilleae are often placed next the Ericaceae. Many Polypetalae are apetalous (*Saraca, Sterculia*) and many Apetalae are polypetalous (*Jatropha* and allied Euphorbiaceae). The Cucurbitaceae, Theaceae and Malvaceae are wholly anomalous in such systems. Engler's divisions, intended as improvements, are more difficult to work, e.g. Parietales with axile placentation.

As generally approved, any system founded on a single set of characters will be unnatural. Both reproductive and vegetative characters are important but, in practice, the herbarium requires the reproductive or floral, and the field requires the vegetative. As an example where the two meet with better understanding, I give *Eugenia* which is extremely difficult to subdivide in the herbarium but which has many, very different bark-characters as yet unconsidered: the herbarium separates widely trees with almost identical barks and, once this resemblance is seen in the forest, the evolution of the species can be perceived, as in the natural group of *E. papillosa, E. oleina* and *E. spicata* with orange, flaky bark.

Unfortunately systematists have created a vicious circle. As flowers are needed to work their keys, they discourage the collection of fruits, not to mention buds, bark, wood, resin, roots and so on, and they are thus unable to accumulate the material which will improve their system. Wood goes to forestry and barks, if at all, to pharmacology, instead of centring under the microscope on the systematist's table. If at first unavoidable, this division of labour requires synthesis.

2. *Ambiguous Description.* Herbarium work gives many characters not observable in the living plant and omits many more not observable in the dried specimen. Thus, it is impossible to understand the common description 'Brown hairy', because many white hairs become brown in drying (*Ophiorrhiza, Ficus*, Lauraceae): in the living state relatively few plants are brown hairy and, thus restricted, the character is most useful. Again, veins may be invisible in a living leaf, and a living leaf may be characteristically glaucous when the dried specimen is greenish, brownish, or blackening according to its age and the manner and state of its preservation, cf. tobacco-leaves. If previous descriptions are copied, I have found that in more than half the cases absurd errors will be repeated, e.g. leaves yellow, brown or black† or veins inconspicuous (when they may be yellow on a dark green leaf); and, particularly, leaves alternate when they are spirally arranged. Further, the size of most flowers and fruits, when taken from dried specimens, do not correspond with the living, e.g. a dried rose or banana.

* *Nat. Pflanz. Fam.* 2nd. Ed., **19a**, 1931, pp. 6, 409 (also Benth. and Hook., *Gen. Pl.* **1**, 416). This example shows the fantastic ideas that can arise in the herbarium, as if, for instance, *Santiria* and *Dracontomelum*, 150 ft. trees, had no other family difference when sterile.

† *Kopsia flavescens, Palaquium xanthochymum, Ixora nigricans.*

Note. The confusion in systematic botany, arising from the study of flattened specimens, between alternate and spirally arranged leaves is most aggravating and displays no understanding of the plant, e.g. *Mangifera* 'leaves alternate' (!). Spirally arranged leaves are borne on upwardly directed twigs which follow, as it were, the shafts of light in the forest, and such trees have spires of foliage, e.g. *Mangifera*, *Barringtonia*, *Palaquium*, *Talauma*, *Dillenia*, *Tristania* and nearly all with doubly pinnate leaves. Alternate leaves, staggered in two rows, are borne by contrast on horizontal twigs thrust *across* the shafts of light and these—the artist's delight—are the sprays of foliage of more modern trees (*Fagus*, *Tilia*, *Cassia* and *Canangium*). The habit may be distinctive almost of families, as in the spirally arranged, pinnate leaves of Meliaceae, Burseraceae, Anacardiaceae, Eucaesalpinioideae and Mimosoideae, in contrast with the alternate pinnate leaves of most Papilionaceae, Cassieae and Amherstieae: or, again, the spirally arranged simple leaves of the Dilleniaceae, Elaeocarpaceae, Sterculiaceae and Sapotaceae, compared with the alternate leaves of the Annonaceae, Myristicaceae and Ebenaceae. In other cases it is generic, subgeneric or even specific, and then nearly allied trees have strikingly different forms e.g. *Eugenia*, *Terminalia Symplocos*, *Sapium*, *Litsea*.

Now since the horizontal spray may be made from alternate leaves (Annonaceae), spirally arranged leaves with displaced petioles (*Litsea*) or opposite leaves with twisted internodes (*Eugenia*) or suppressed upper leaves (*Randia*, *Argostemma*, *Geunsia*, *Sonerila*) and ascending spires may be made from spirally arranged, decussate and whorled leaves (*Alstonia*, *Dyera*), it is obvious that we want new terms to describe these two extreme ways of carrying foliage. I suggest 'foliage applanate' and 'foliage ascending'; thus, for example in the Lecythidaceae:

applanate foliage: *Lecythis*, *Bertholletia*.
ascending foliage: *Gustavia*, *Couroupita*, *Barringtonia*.

As complications, *Fagraea fragrans* (Loganiaceae) has ascending foliage on hanging twigs in the manner of a weeping willow but *Pterocarpus indicus* (Papilionaceae) has applanate foliage, while saplings of *Cassia* have applanate foliage on ascending twigs. And there is the phenomenon of Terminalia-branching giving short spires of ascending foliage on applanate branch systems so that one sees from above a carpet of leaves and, from below, the supporting skeleton of twigs and branches; and these branch-systems, being set in tiers on the trunk, give the strange appearance of what I have called pagoda-trees,* e.g. *Terminalia*, *Sterculia*, *Elaeocarpus*, *Ceiba*, *Alstonia*, *Palaquium*, *Alseodaphne*.

Actually we need a solid geometry of tree-form to show how systems with apical growth and axillary branching, rooted in the ground and displaying foliage, pervade space.

3. *Synonymy*. The political isolation of botanists in neighbouring tropical countries and of systematists dealing with adjacent tropical floras in temperate countries has introduced an enormous burden of synonymy. There is still a vast amount of hack-work to be done before the common plants of the Indo-Malayan region (India to tropical Queensland, South China to Christmas Island) have been given their correct botanical names: yet, nothing is more exasperating for botanists, professional or amateur, than a book with incorrect nomenclature.† The position is obscured, even more, for the botanist by the modern tendency to split genera into geographical units, e.g. *Ormosia* and *Afrormosia*, *Carapa* and *Xylocarpus*. The effect is that tropical botanists use vernacular names in preference to the dubious botanical and thus reveal an absurd side to learned systematy.

* *Wayside Trees of Malaya*, p. 30.

† So I found that the botanical names of many common Malayan trees had to be changed to earlier synonyms, even the common village tree 'Chempedak' had been confused with the common Jack-fruit, to which the botanical name of the Chempedak (*Artocarpus integer*) had been given. Yet *A. integer* had been proposed as a *nomen conservandum* for the Jack-fruit in ignorance of the Chempedak. The common species of *Aphanamixis* (Meliaceae) has a different name in India, Malaya, Java, Borneo, the Philippines and New Guinea (and thus, incidentally, shows how mistaken may be the high endemism ascribed to many Eastern floras). Nearly every expedition to the New Guinea region has discovered new species of *Archidendron* (*c.* 25 spp.) without recognizing the old. Still to be proved are the correct names of many common beans, crucifers, spinaches, pandans and aroids cultivated in tropical Asia, and of the wild bananas, to mention a few striking examples. Are we even sure of the botanical names of the Rubber tree and Royal Palm? One would have thought that leading herbaria could have established the names of these common plants.

4. *Error.* A common and serious defect of existing tropical floras has arisen through the copying of family and generic characters from other works without careful definition for the subject flora. Thus common plants often do not have the family characters, e.g. Malvaceae under Polypetalae with the sympetalous *Hibiscus* as its commonest member or Euphorbiaceae under Apetalae with the 5-petaled *Jatropha*. As a principle, in the present state of knowledge, copying should be avoided because it involves a change of context to which the original words may scarcely be applicable or not at all.*

Thus, contrary to my early belief, I found the systematic work on Malayan, if not Asiatic, flowering plants incomplete and unreliable and so unsuited to the identification and study of the living plants that nothing could be accepted without personal verification. The introductory, semi-popular book on common trees had to be preceded by some 300 pages of systematic botany (*Gard. Bull.*, S.S., 1939–40), during the preparation of which I became aware of what I must call the enormous humbug of tropical botany. For the benefit of others who may likewise be dismayed by the grandeur of so many unfamiliar families and genera, and thereby deterred from contributing to this branch of botany, which is so much in need, I would say that the names indicate mostly a mass of imperfectly sifted raw material, much of it non-botanical, awaiting refinement by those who can study the living plants. To bring tropical botany to the present level of temperate botany, there is needed yet in the tropics a hundred times as many botanists as the world has ever known.

Note. Few, if any, of the macroscopic terms of systematy can be construed microscopically, as modern botany requires. Thus, 'leaves coriaceous' may imply thick cuticle, thick epidermal walls, hypodermis, sclerenchyma, idioblasts, thick mesophyll or another microscopic feature causing toughening of the blade. Again 'seeds red' may refer to aril, testa or placental envelopes. Again, 'stamens many' places *Paeonia* with centrifugally developed stamens in the Ranunculaceae which have centripetally developed stamens, rather than in the Dilleniaceae with centrifugal stamens. Thus, systematy is still at the level of the pocket lens and the tendency is to leave the systematist in the herbarium at the Linnean level and to transfer the anatomist, with the modern microscope, to the laboratory. The systematist becomes involved in the same vicious circle. Microscopists tend to justify their laboratories by the elaboration of special 'techniques' and the systematist becomes severed still further from the instrument that he most needs: for only the microscope can make a real science of systematy.

The botanist educated in a north-temperate country, on coming to live in the tropics, soon has to unlearn his special teaching. Plants are 'cold-blooded', as are most animals, and so they are more active in the warm climates and have there evolved into their greatest complexity. Botany has grown up in wintry climates and its general text-books omit the majority of plants which do not winter. It has accepted principles which to the tropical botanist must appear as secondary phenomena: for example, the anemophily of *Quercus* and other minute-flowered trees, the success of the Compositae as the most highly evolved flowering plants, the value of the large, coloured flower for insect-pollination (cf. *Gentiana* compared with an entomophilous Macaranga with minute green flowers), the importance of the ecological sere, the primitiveness of Ranunculaceae and Alismataceae, and the deciduous habit among extra-tropical trees. To the tropical

* These errors abound in the *Flora of the Malay Peninsula* (5 vols., 1922–26), with so many others, however, that the work is useful mainly as a list: cf. Symington, *Kew Bull.* (1937), 318, and Corner, *Journ. Mal. Br. Roy. As. Soc.* (1933), 42.

botanist, anemophily is rare and spells paucity of insects; Compositae are insignificant and cannot compete with the main mass of tropical vegetation; any scented speck will attract an insect; the sere is trifling in a continent of forest, unless evolution be the sere of the future; no herb can be primitive: there are, specifically and generically, more deciduous trees in the tropical 'evergreen' rain-forests than in the temperate deciduous forests. So, too, one believes that *Cycas*, *Gnetum*, *Agathis*, *Gleichenia*, *Dipteris*, *Angiopteris*, *Helminthostachys*, *Marsilea*, and *Lycopodium cernuum* are rarities or oddities, in the same way as the place of the large and varied *Podocarpus*, or coneless conifer, is taken by the monotypic yew. No other science is so dependent on its tropical material as botany, not even zoology for heterotrophic organism does not feed directly upon the light, and, thus, through the neglect of its tropical aspect no other science is so undeveloped. As a principle, every subject of botany should be studied from its unspecialized tropical aspect if it is to have its proper scientific background.*

The modern expansion of civilization has made the large and hazardous expedition to the tropics a thing of the past.† We must look forward to and plan the development of botany in every aspect in tropical institutes. At once the problem arises whence will come the books, for without books there can be no science and lack of them is the main handicap of the tropical scientist. The problem must be faced and overcome.

First, there is no reason why research should be held up because the botanist is unable to consult earlier investigations, and priority matters not in the pursuit of truth. The fact that the earlier studies are not available over half the world proves that more publications are needed and that botanists resident in the tropics must build up a new literature of tropical botany. How much original research has lain unpublished for this reason cannot be guessed but it has been a great loss. One must, therefore, advise young botanists brazenly to face the situation and to ignore, of necessity, what they cannot possibly obtain, through no fault of their own, from distant libraries. Good descriptions and large, detailed drawings of nearly every tropical plant, made from living material, particularly in microscopic detail, are everywhere needed and independent repetition of research will be both unavoidable and desirable, especially if physiological, for the establishment of knowledge.

Secondly, the second World War has destroyed so many libraries and collections that it is surely time to take stock and to re-arrange the background of botany. Few will be able to consult the early periodicals, the early books and the type-specimens. It behoves botany, therefore, to prepare monographs which shall be fully descriptive, historical, theoretical, referenced and cross-referenced and illustrated by copies of every good drawing that has been published.‡ Thereby every subject will be brought reasonably

* Whether it be physiological, morphological, cytological, ecological or systematic. Thus, the cytology of cereals must have the cytology of bamboos in the background, just as with their morphology: and the existence of many xerophytic mechanisms, as resin-coatings, dense tomentum, geophilous habit, deciduousness, thorniness, and so on, in tropical freshwater swamps, must be considered in the evolution of plant habitat-forms.

† Truly hazardous would be an expedition of tropical biologists to a temperate country. For, if Guttiferae, *Caulerpa* and monkeys can be studied in northern latitudes, arctic lichens, laminarians and migratory birds would make delightful pastimes in the tropics. I do not know which is the more dangerous, tropical nature or temperate man.

‡ Monographs, for instance, on cuticle, epidermis, stomata, leaves, pigments, tannin, floral development, embryo-structure, families, genera, species (as the tapioca, mango, or banana plants), nuclear structure, micro-manipulation, experimental embryology, hybridization, parasitic physiology and so on. The encyclopedia may run to a few thousand volumes, and thus become a reasonable nucleus for a laboratory.

up-to-date, as a foundation for new knowledge, and thereby a new institution will be able to acquire such an encyclopedia of botany as the nucleus of its library, instead of waiting opportunities to buy at great cost rare books of little general use. Moreover, what is not in the encyclopedia may be taken as unknown and fit for publication. The labour of preparing the encyclopedia may seem enormous but it cannot much exceed the energy spent yearly, in the aggregate, by botanists throughout the world 'looking up references'. This, I suggest, is the contribution which the large botanical libraries should now make to their science; failing which, they will surely be ignored and all their learning trapped.

In revealing some defects of botany, I hope to have shown how it should progress in the reconstruction of the world which is about to take place.

1. There is urgent need for collecting not merely dried 'systematic material' but also anatomical material, with detailed field-descriptions and, if possible, paintings, *where forest is being felled.*

2. There is urgent need for the preservation of the tropical forest, particularly *lowland*, in large nature-reserves *in all tropical countries*, free from any commercial exploitation as logging, mining, hunting and so on. If science is universal, botanists should co-operate in preserving the still wonderful heritage of the tropical forests.

3. More official botanists and temporary research workers are needed in the existing tropical institutes. And it should be possible for these botanists to return, if desired, to the temperate institutes.

4. The number of Botanic Gardens in the tropics should be increased and should develop better relations, particularly in the loan or exchange of staff.*

5. A Botanical Encyclopedia is required to spread existing knowledge over the earth.

To young botanists in the tropics I offer the advice given me by A. H. Church, of Oxford University, 'Draw everything, photograph everything, note everything'. None can succeed, but only with such intention can one accumulate through the years first-hand information for maturer thoughts. So much happens in the tropics in so short a time that most is over before it is perceived, and only by repeated observation and revisiting of the same places can one begin to grasp what is happening. In particular, one should study living tissues with the microscope and be satisfied with no description that is not microscopic: trees and palms, as well as algae, should be conceived in terms of cells. So one remains aware of much that is easily forgotten, for instance the position and nature of pigments, the development of aerenchyma, the abundance of tannin, the rapid respiration of tissues, the activity of so-called resting nuclei in maturing cells, and the functions of the epidermis: if sections are cut, moreover, under the binocular microscope, one can feel the different tissues as they are severed and can perceive the mechanics of the plant. Lastly, no structure can be understood unless its manner of development is known: embryology, or organogeny, is the root of biology.

* It is apt to be overlooked that botany covers forestry, horticulture and the greater part of agriculture. A Botanic Garden is usually considered an unnecessary adjunct, which is reflected in the diminishing personnel. Actually, the Botanic Garden is the tropical counterpart of the Botanical Department of a temperate university: it has grown up before the need for the university and resembles, thus, the tropical museum which is the zoological-ethnographical counterpart of schools of zoology, anatomy, anthropology, etc.

THE PROSPECT FOR POLLEN ANALYSIS IN THE STUDY OF THE EARTH'S CLIMATIC HISTORY

By LENNART VON POST

Geological Department, University, Stockholm

BEING THE VEGA LECTURE DELIVERED ON 24 APRIL 1944

(By permission from the Swedish Journal *Ymer*, 1944)

(With 13 figures in the text)

First of all let me tender my sincere thanks to the Swedish Anthropological and Geographical Society for honouring me with the most illustrious scientific reward at its disposal. I myself know best how little I deserve the Vega Medal. The greatest part of what I could and should have done to bring the problem of changes in climate after the ice age nearer solution remains unaccomplished, partly because the time has been too short, but also, unfortunately, to no small extent, because of my own lack of enterprise. Fortunately, however, colleagues both in Sweden and elsewhere have considered it worth while to take up the work. It is due to these known and unknown collaborators that we have succeeded in making some progress along our path. I look upon the mark of distinction I have just received as an honour not personal, but rather as one paid to our branch of science. For these reasons I felt able to accept the extraordinary honour of having my name inscribed among the Vega medallists.

I think it suitable this evening to look ahead, to give some indication of the many problems that remain to be cleared up before the climatic history of the world can be considered as being near the definite elucidation of its course, or the interpretation of its purport, at least concerning the periods of thousands of years after the last glaciation. But we must first see what has been accomplished up to the present time.

The Blytt-Sernander scheme of climatic change

Research into the history of climate is, as far as the post-glacial period is concerned, essentially Swedish, both in the defining of the problems and the methods employed. Rutger Sernander, the Wahlberg medallist of our Society, is, in this department of science, the great man and pioneer. Inspired by Axel Blytt's *Essay on the immigration of the Norwegian flora during alternating rainy and dry periods*, which was published in 1876, Sernander began at the close of the 'eighties to investigate some central Swedish peat bogs. He found in them a correspondence to the series of periods that Blytt regarded as being recorded in Norwegian bogs. Thus came about the Blytt-Sernander scheme with its four post-glacial periods of climate (Fig. 1). The odd ones of these reckoned from below, the 'boreal' and the 'subboreal', were continental, and in the bogs were represented by 'stump layers'; the even ones, the 'atlantic' and the 'subatlantic', had

had a more maritime, humid, climate and corresponded to layers of peat formed under damp conditions. But the climatic significance of the 'stump layer' was at first almost universally disputed. As many may still remember, it was particularly the young Sernander's competitor in the arena of peat-bog investigation, our Society's excellent secretary, Gunnar Andersson, who impugned vigorously the theory of climatic fluctuations. Gunnar Andersson acknowledged only the post-glacial warm phase, of which he himself found such abundant evidence in the fossil plant and animal remains of the peat bogs. Right on into this century there was only a small circle of Uppsala biologists who supported Sernander's view. It was with the Geological Congress in Stockholm in 1910 that his views won the field in Sweden; and from 1923 one may say that the ideas of the 'Uppsala school' began to strike root practically all over Europe. For it was then that there appeared the treatise by Helmuth Gams and Rolf Nordhagen, in which these investigators demonstrated that, even in southern central Europe and the Alps, there could be traced post-glacial changes in climate similar to those that Blytt found in the Norwegian peat bogs and Sernander discovered in those of Sweden.

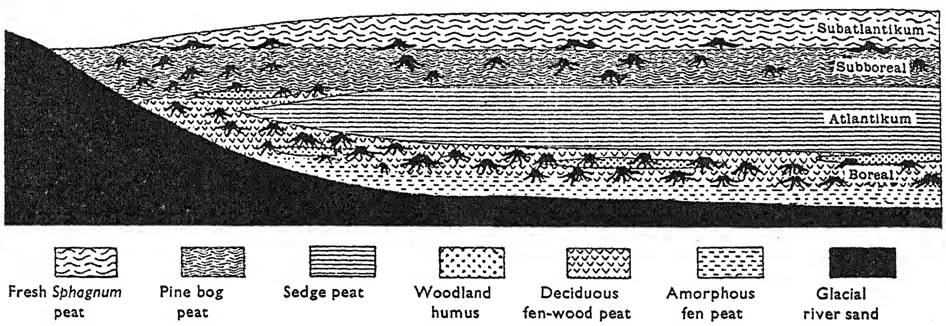


Fig. 1. Somewhat schematized profile through a part of the edge of Lerbäck Bog in Närke. Lerbäck Bog is a 'spring bog', that is to say, the peat formation is brought about by ground water running on the surface. The changes in intensity in this flow of water have been clearly registered in the sequence of layers in the bog. Drier periods are represented by both the woodland peat layers, damper phases by sedge peat between the 'stump layers' and by *Sphagnum* peat highest up in the series. The bog is one of the first that Rutger Sernander investigated, and it shows beautifully the Blytt-Sernander sequence of periods registered in the series of peat beds.

Sernander had succeeded in dating his sequence of periods both by connecting them with the changes of land level in Sweden after the ice age and also by means of the archaeological time scale. He fixed his 'atlantic period' at the time about and immediately after the advance of the sea, which, within the Baltic area, is known as the *Littorina* maximum. The 'subboreal period' corresponded approximately to the bronze age and the 'subatlantic' to the iron age. Throughout the boreal, atlantic, and subboreal there extended the 'post-glacial warm period', a wave of heat lasting several thousand years, which caused *Trapa natans* to become one of the commoner plants of the lakes of south Sweden, which permitted the hazel to grow and set fruit far to the north of its present northern boundary, and drove the forest up into our mountains 300 m. above its present limit. According to Sernander the warm period reached its peak in the subboreal period; and the boundary between this period and the following subatlantic one corresponds to 'the great post-glacial climate deterioration', a catastrophe which not only put an end to the warm period, but which also ushered in the 'fimbul winter' during the centuries

just before the birth of Christ. The climate must then have been considerably colder and more rainy than at present. This phase must have been so severe in Scandinavia that the crops failed year after year, and the inhabitants, driven by famine, sought a home in more southern countries. Sernander sees here, and many geologists and archaeologists agree with him, the chief cause of the migrations of the Germanic peoples. The subboreal-subatlantic boundary in the sequence of layers in the bogs forms usually a sharp contact between a lower bed laid down under dry conditions and an upper one which bears witness to great humidity on the bog surface. This contact has been named the boundary horizon, 'der Grenzhorizont', following the usage of C. A. Weber in Bremen, the German pioneer in the investigation of peat bogs.

Erik Granlund's recurrence surfaces

Intensified investigation of peat bogs has, in later times, made it clear that Sernander's scheme does not, by a long way, contain the whole truth about post-glacial climatic changes, even in its main features. The portrait of these changes, whose outlines now begin to take shape, is clearer and easier to grasp if looking at the principles of their development, but at the same time they appear considerably more complicated in their structure. In the year 1932 Erik Granlund was able, chiefly on the basis of the material brought together at the peat inventory of the Swedish geological survey,* to show that the Swedish raised bogs contain not only the subboreal-subatlantic boundary horizon, but also a whole series of such 'inversion contacts' both older and younger than the classical one at the boundary between the bronze age and the iron age. He called them recurrence surfaces, for they indicate setbacks in the spontaneous development of the bog towards drier and drier conditions. These recurrence surfaces portray repeated changes from a dry continental climate to a damper and more maritime one and vice versa. There had occurred, according to Granlund's evidence, at least two 'subatlantic' climatic phases during Sernander's subboreal period and after the fimbul winter of Sernander the climate had twice changed over to the 'subboreal' type and then again to the subatlantic, the latest of these changes falling about A.D. 1200–1300. The datings were made by means of pollen diagrams, into which archaeological findings of known age were fitted. But reasons were found to suppose that the series of recurrence surfaces continued backwards beyond the oldest of those differentiated by Granlund. This recurrence surface is dated at the passage-grave period, i.e. about 2300 B.C., according to the chronology of Oscar Montelius.

Granlund's work showed that the post-glacial warm period did not end abruptly with a climatic catastrophe about 500 B.C., as supposed by Sernander; but that instead of this event we must suppose a gradually advancing climatic deterioration spread over at least 4000 years. This process was, however, not continuous. Just in the same way as, during autumn, summer gradually changes to winter during repeated alternations between days of summer weather and wintry cold, so the climate curve falls and rises from the warm period to the present time, through the bronze age, iron age, and our so-called historical time, swaying between fimbul winters and phases which were echoes of the glorious climate of the stone age.

* A survey of the peat resources of Sweden made for the Government in 1916–22.

Pollen diagrams

In what has been said about the course of the climatic deterioration I have to a certain extent anticipated the evidence of pollen analysis about climatic changes after the ice age. Pollen analysis in its present form, or, as it should be properly called, pollen statistics, since the fundamental principle of the method is quantitative, was designed mainly to serve as a means of determining geological time. The method is based on the well-known fact that the pollen of certain plants is caught up by the wind and carried far and wide, eventually to fall again as a fine rain of dust. An insignificant fraction reaches its goal, the stigmata of the plants; but by far the most of it falls on the ground and rots away.

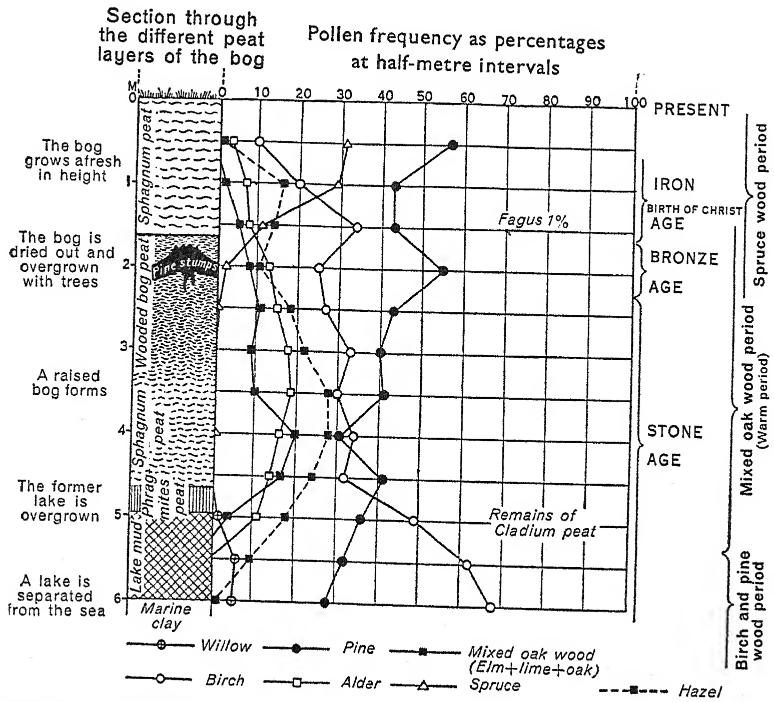


Fig. 2. Pollen diagram of Nyckel Bog near Östra Laxsjön at Tiveden between Laxå and Askersund in Närke. The bog developed by the overgrowth of an ancient lake, and in its sequence of beds the subboreal-subatlantic horizon is a sharp contact between a strongly humified wood-moss peat and an almost unhumified *Sphagnum* peat formed under the influence of copious precipitation on this raised bog which in course of time replaced the original lake. The pollen diagram is typical of central Sweden and shows a threefold division of the post-glacial woodland development: first a phase with almost exclusively birch, pine and willow, after that a period in which the forms requiring heat, mixed oak wood (i.e. oak, lime and elm), alder and hazel, luxuriated together, and lastly, approximately from the boundary horizon onwards until the present, a 'period of spruce wood'.

Some naturally finds a resting place where new deposits are in process of formation, and because of the chemical resistance of the pollen grains it comes about that in the peat of bogs, in the nekron mud, clay and sand of inland lakes, and in the ooze of marine bays, samples of the pollen rain of the district are preserved. In this pollen rain is reflected, to a certain degree, the average composition of the vegetation of the region, specially of woodland, and by examining statistically a series of beds, layer by layer, the fossil pollen

rain, which composes the 'pollen floras' or 'pollen spectra', of the respective layers, we can follow from period to period the changes in the woodland geography of the region. If we analyse in this way deposits the age of which is ascertained either by archaeological findings in them, or still better by Gerard De Geer's geochronological method, we can obtain, so to say, time labels which can be transferred to other pollen-bearing formations that we wish to date. Nevertheless the inescapable basis of this chronological apparatus is the establishment of the historical course of the development of the vegetation, as this appears in the pollen diagrams. For many pollen analysts this is the only goal, and this point of view, that pollen analysis can become an aim in itself, is by no means to be rejected, for its immediate result, the curves in the diagram of the change in frequency of the different elements of the vegetation, is neither more nor less than the most complete and most realistic register of climatic fluctuations throughout the past which we now have at our disposal.

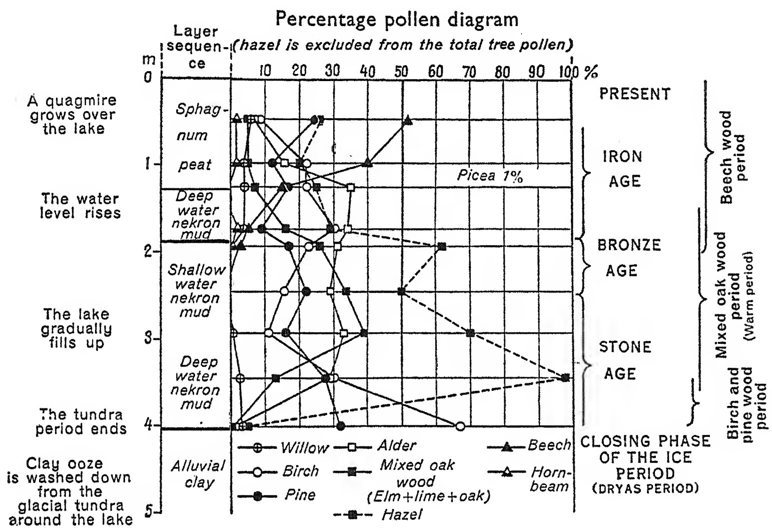


Fig. 3. Pollen diagram of Bjärsjölagård Bog between Mt Linderödsåsen and Mt Romeleåsen in Skania. The analysed series of samples is taken in a recently overgrown lake, which, in the course of time, has been filled with nekron mud of various kinds, and at length has been covered by a quaking bog. The subboreal-subatlantic contact lies in the nekron mud scarcely 2 m. under the surface of the quaking bog and indicates a considerable heightening of the water-level of the lake. Immediately below this boundary horizon the pollen curve for the beech begins in the manner characteristic of south Sweden. The beech is accompanied by a small amount of hornbeam and also, in this case, willow. Spruce, on the contrary, is almost entirely absent in the pollen diagram of these tracts. In its place a period of beech wood here follows the period of mixed oak wood, i.e. the warm period.

Fig. 2 shows a typical pollen diagram from central Sweden, in fact from Närke. This diagram is one of the first that was made, and it is now almost exactly 30 years old. We see how the curves for the woodland trees of the warm period—the mixed oak forest trees, and also alder and hazel—begin, reach their climax and fall. We see how the pollen curve for the spruce sets in immediately below the subboreal-subatlantic boundary horizon and goes on rising towards the present time. The spruce has invaded these tracts under the influence of the climatic deterioration. Let us take, as another example, the first of all my pollen diagrams, one from Skania (Fig. 3). In principle we have just the same woodland development as in Närke, but with two differences: (1) that the curves for the warm

period, because of the more southern position, attain double the height they reach in the diagram for Närke, and (2) that the spruce is missing. Yet, its place is taken by a beech curve similar in form and position but considerably stronger. These two diagrams only tell us, over and above what was already known of post-glacial forest development, that the beech in Skania occupies historically a similar place to the spruce in the north, so that beech thus did not invade its present area in Sweden until the era after the warm period. Beyond this, it was by its firm grip on the phenomena that pollen analysis, from the very first, obtained precedence over the old method based on so-called macroscopic fossils, i.e. fruits and seeds, leaves and remnants of wood. We shall soon see that its precedence is significant.

Revertence and regional parallelism

I have mentioned the woodlands of the warm period and the woodland elements of the time of the climatic deterioration as if it were a self-evident fact that the changes in woodland plants witnessed by pollen diagrams were brought about by causes having to do with the history of climate, but many attempts have been made to find other means of explanation. It has been suggested that a gradually increasing soil exhaustion for a certain species of tree might have given another competing species the upper hand, or that some species, because of their special means of distribution, might have been able to make way earlier than others, or that a progressive impoverishment of the soil by weathering may have taken place through the ages, etc., and theoretically such explanations can by no means be thrust aside. There have, however, long been found, in results of pollen analysis, two pervading features, each of which binds together unquestionably the history of the woodlands after the ice age and that of the climate. They are what I call revertence and regional parallelism.

Revertence consists in the fact that the same elements of vegetation that characterized the oldest phases, but receded during the middle stages, recur as characteristic forms towards the present time. My example (Fig. 4) is from Gotland and shows a compound revertence of that kind. At the bottom pine is dominant. Upon the pine zone follows a zone with large increases in the frequency of birch, and after that the peak development of the mixed oak forest trees and alder. In the upper part of the diagram the same series appears again but in reverse order. I, for my part, know of no natural factor possessing sufficient faculty of changing to bring about this rhythmic course of development except a wave of climate which at first gradually rises and then just as gradually sinks away.

If possible, climate shows itself still more clearly as a decisive feature in the development of woodland in the phenomenon of regional parallelism, which implies that the same scheme of structure recurs in pollen diagrams within one plant geographical region after another, but that every stage of development is represented by different plants within each of these regions. Our two diagrams from Närke and Skania have already given examples of regional parallelism, and the diagram from Gotland forms a third link in the chain with pine as a substitute in the youngest stages for spruce and beech in the diagrams of the Swedish mainland.

Revertent pollen diagrams are found in nearly all the regions of the earth which have been investigated by pollen analysis, and we shall soon find that regional parallelism too is a general law, not merely within our country from Kiruna to Ystad, but over the whole of Europe, indeed very likely all over the globe.

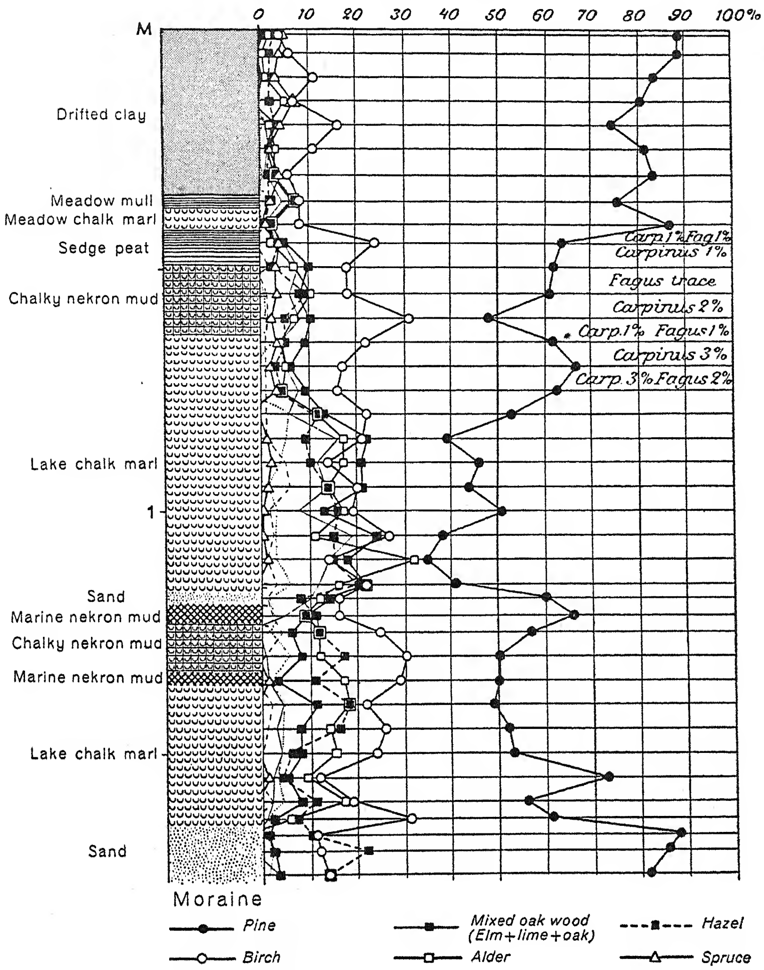


Fig. 4. A pollen diagram which shows 'revertent' forest development. The peak of the species favoured by the warm period are both preceded and followed by a phase in which pine dominates almost completely. Both the beech and the spruce play quite an insignificant role even in the latest stages of development. But the pine has come in their place, so that in the last stage of development the woodland conditions become nearly the same as they were at the beginning phase. Upwards as well as downwards there are stages with abundant birch intercalated between mixed oak-wood period and the phases with pine wood. And so we have a course of development with two-fold revertence. The diagram is typical of such regions of Gotland where the soil is made fertile through a bed-rock of marl-stone.

Europe

Fig. 5 contains a 'diagram chain' from different latitudes within our lengthy country. The curves are arranged so that the total sum of deciduous tree pollen (excluding, however, the beech and *Betula tortuosa*) appears in collective contrast to the frequency of conifers, and also, sometimes, to that of the beech, *Betula tortuosa*, and the willows. Furthermore, the diagrams are 'synchronized', i.e. the scales of height are harmonized so that portions of the diagrams of like age, independently of the actual thickness of the beds analysed, lie level with one another throughout the chain. The diagram chain cuts through all the plant geographical provinces of Sweden from the region of beech wood in the south to

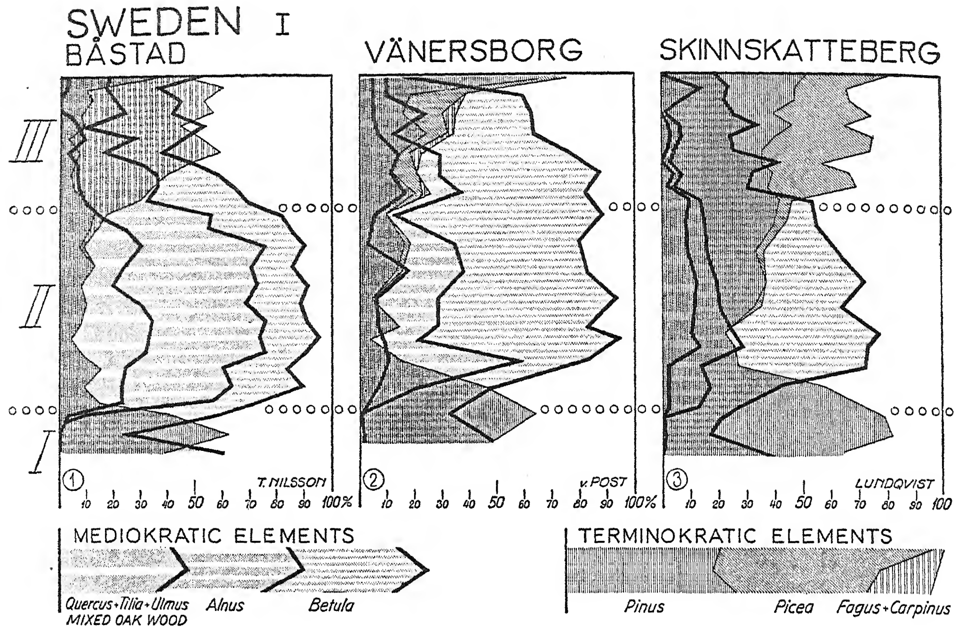
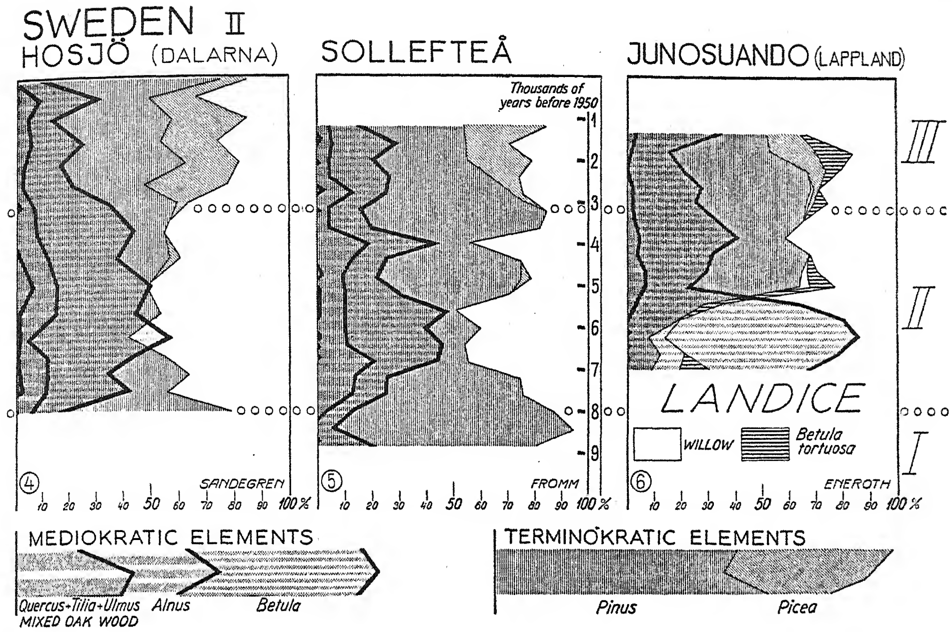


Fig. 5. Synchronized pollen diagram chain through Sweden from Mt Hallandsås to north-east Lapland. Among the 'mediokratic' elements of the pollen flora, the forms of the warm period, birch plays a considerable role which increases proportionately more and more towards the north. Already in southern Norrland the pollen of the mixed oak wood ceases to form coherent curves, and in the north this element disappears entirely. The birch pollen in all the diagrams can with certainty be supposed to belong practically exclusively to *Betula verrucosa* and *B. pubescens*. In Junosuando Bog, the diagram of which was worked out at the Geological Department of the University at Stockholm by Prof. Olof Eneroth of the Forestry College, by statistical analysis of the size of the pollen grains, the presence of both *B. nana* and *B. tortuosa* was ascertained. In the diagram the former is excluded; the latter is accounted for among the terminokratic elements. The hazel curve is left out. In the synchronization the following standard levels are used: (1) the beginning of the alder curve, (2) the peak of the mediokratic pollen curves, and (3) the incipient rise of spruce, or, as the case may be, beech.

the boundary zone between the north Swedish region of coniferous wood and the *regio subalpina* in the north. First of all we notice revertence, through the pine curve, in several of the diagrams. Secondly, we are struck by the manner in which, in the middle parts of the diagrams, the pollen frequencies of the mixed oak forest trees gradually decrease towards the north, eventually to disappear altogether. In the same measure as the mixed oak wood, together with alder, loses in quantitative significance, the birch takes their place as an element characteristic of the middle zone. At the same time as the oak and its satellites were spread far to the north of their present northern boundaries, birch wood of the type which, in our time, forms the chief mass of the deciduous woods of central Sweden, had, more or less, right up into the most northerly parts of Lapland, the upper hand over the coniferous wood which both preceded and followed the phase of birch wood. If we look also at what happened after this period of deciduous wood all over Sweden we then find, as new invaders during the phase of development from which the present state of things arises, not only the beech and the spruce, but also, in the diagram from Lapland, *Betula tortuosa*, each of the three within its own region as determined by the climate of to-day.

Let us proceed southwards to the Alps. The diagram chain (Fig. 6) contains examples



The diagram from Sollefteå has served as a vertical standard scale. This is worked out at the Geological Department by Erik Fromm on series of samples from the post-glacial sea fjord and river sediment in the valley of the Ångerman River, which were collected and determined geochronologically by Ragnar Liden. From the original diagrams, by interpolation, the value for each 400th year has been selected, and in the diagram from Junosuando a corresponding scale of intervals is used for the pollen spectra likewise selected by interpolation. In the rest of the diagrams, according to the density of the original diagrams, there have been selected every second, every third, or, in some, every fourth or every fifth analysis, so that the density of the analysis in the diagram of the chain becomes approximately equivalent throughout the whole series. In the sequence in layers of the bogs this density corresponds on an average with a $\frac{1}{4}$–$\frac{1}{2}$ m. The approximate correctness of the synchronization is confirmed by a large number of archaeological findings in southern Sweden worked into pollen diagrams.

from Scotland, Denmark, northern, central and south Germany, and Switzerland. Differences from the Swedish diagram are slight. In the central portions, however, both the alder and the birch are gradually suppressed so that the mixed oak wood in places becomes almost totally dominant, and in the upper section there entered, in perfect correspondence with the young beech wood and spruce wood of Sweden, *Calluna* heath in Scotland and *Abies pectinata* in the central European mountain tracts. We could go even farther. Then we should find on the south side of the Alps *Castanea vesca* occurring in the same manner, in eastern Russia the Siberian conifers, *Abies sibirica*, *Larix sibirica* and *Pinus Cembra*, and, similarly, in Ireland birch and hazel. Also, far up in the north, the arctic tundra, as Finnish and Russian investigators have shown, has in recent time advanced its boundary to the south at the cost of the former pine wood. Even in these widely separated parts of Europe we meet revertence as a constantly recurring feature in development.

The diagram from Scotland deserves a moment's special attention. It belongs to a small collection, from various parts of Scotland, worked out in 1936 at the University's Geological Institute in Stockholm by Dr George K. Fraser of Aberdeen. Circumstances prompted us to make these diagrams according to a principle new for Europe. The usual rule is to reckon the percentage of pollen on the sum total of tree pollen, and in this figure

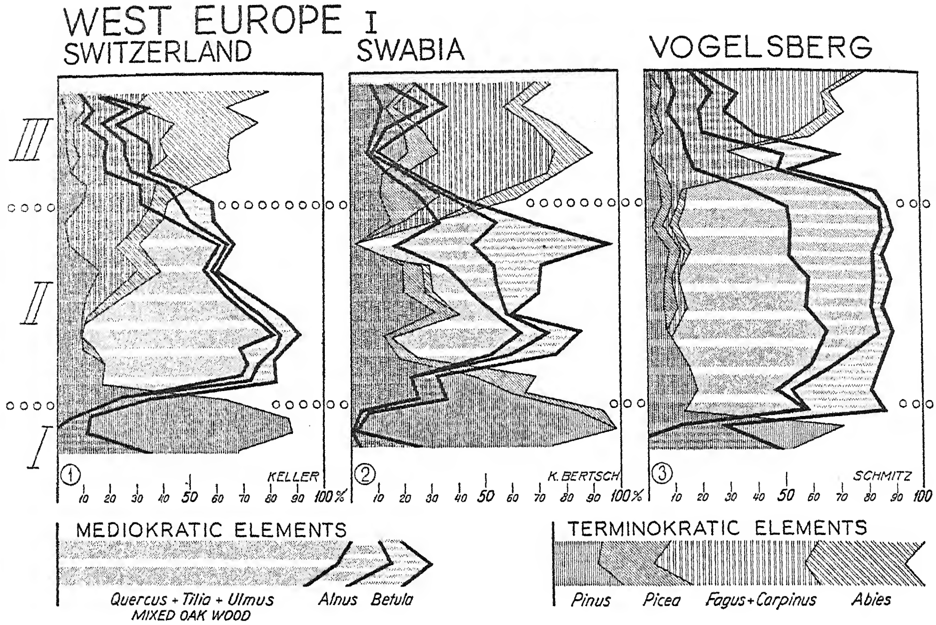
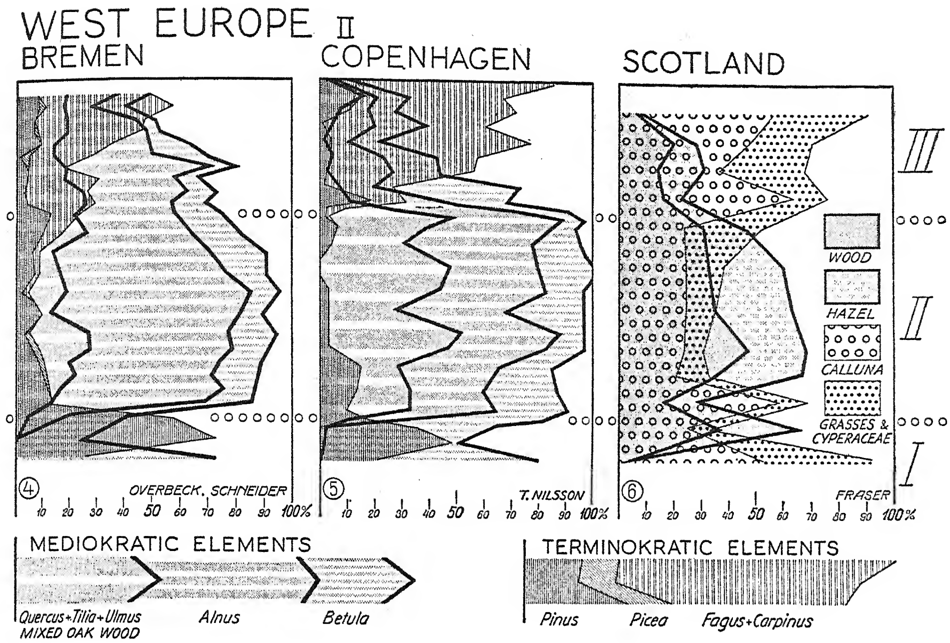


Fig. 6. Synchronized pollen diagram chain through west Europe. The chain forms a direct continuation of the diagram chain from Sweden. According to the law of regional parallelism, the mixed oak wood towards the south becomes still more dominant among the mediokratic elements; and in the same way as the beech in the maritime districts of southern Sweden, during period III, takes the place of the continental spruce, the southern silver fir comes in. For the diagram from Scotland refer to the text, p. 9. The synchronization

(100) to include neither hazel nor such elements as *Calluna*, grasses and sedges. If we dealt in this way with the Scottish material we obtained, true enough, diagrams which showed a very beautiful revertence for pine and partly also for birch, as well as in the middle portions the usual peak of mixed oak wood and alder, but the diagrams thus constructed evaded the essential point in the problems about the vegetation evolution of Scotland, namely, that of the mutual changes in frequency of heath and woodland. In order to obtain a direct answer to this question we tried the type of diagram which now represents Scotland in my diagram chain through western Europe. In this diagram have been contrasted, as vegetation elements equivalent from the ecological point of view, woodland, hazel scrub, and heath, the last-named represented by *Calluna*, grasses and sedges. We see how manifestly the woodland as a whole, together with the hazel, in Scotland corresponds historically to the more warmth-loving species of trees in other parts of Europe and how representatives of the heath constitute the revertent component. An evolution similar to that in Scotland is confirmed within other west European heathlands, e.g. north-west Germany and Vestland in Norway; and from Sweden too pollen diagrams are published, from Bohuslän by Per-Olof Atlestam, which, rightly interpreted, prove the same historical status for *Calluna* heath.

Mediokratic and terminokratic elements

Revertence is the leading theme in the evidence of the pollen diagrams of west European woodland development after the ice age. The theme varies from district to district, and it can even be veiled by the effect of local factors; but the variations are always controlled



is carried out in the same way as in the Swedish diagram chain. Here, too, Fromm's geochronological diagram from Sollefteå is used as the standard scale; and also from Denmark, Germany and Switzerland, there are sufficient archaeological data in the diagrams for the time co-ordination to be considered fairly certain. But, in the nature of the case, the Swedish time scale can apply only approximately to continental pollen diagrams. In order to determine the exact synchronization continued precise investigations are needed.

by the law of regional parallelism. If we look only at the letter of the law and refrain from seeking its meaning, the principle can be thus expressed: the elements of the fossil pollen flora are divided into two main groups. One of these, which I term the 'mediokratic', has more or less marked preponderance in the middle phases of the development, and it is both preceded and followed by the elements of the other group, the 'terminokratic'. We can speak of single or double terminokrata according as to whether revertence is more or less marked, and we thus obtain, empirically, a division into three of the post-glacial woodland development, which is as general as it is unescapable, with stages I and III characterized by terminokratic elements and stage II by mediokratic ones. There thus appears, without theoretical explanations, the development scheme of woodland history, which the pollen statistic investigations reveals for Europe. This scheme has indeed proved just as adequate outside Europe also.

Now is it conceivable that anything other than climatic changes could have brought about this general and, within certain regions, fundamental transformation of the forest distribution of our part of the world? Nay, if we turn, for the moment, our attention from the considerable displacements in east to west direction between continental and maritime conditions which the pollen diagrams also register, then we recognize an ancient consistent displacement of the entire woodland geographical regional system of Europe, first towards the north and after that towards the south. From pollen analytical data and from concordant discoveries of plants and animals we can approximately determine the measure of this latter migration as about five degrees of latitude, and we

must unquestionably conclude that the general rate of temperature of our part of the world, at the peak of the mediokratic woodland elements, was, in corresponding degree, higher than now. The existence of the post-glacial warm period in the northern countries is, thus, further confirmed by pollen analysis. Its effects on woodland geography have been defined, and the scene in the drama of climatic history has been widened so that it is now enclosed by the Urals and the Atlantic, and by the Alps and Arctic Ocean. It is now quite 20 years ago that attempts were made, with pollen diagrams as a basis, to draw 'fossil woodland maps' for the chief phases of the post-glacial epoch, and in 1935 Prof. Wladyslaw Szafer in Cracow actually regarded the time as ripe for the introduction of 'isopollen lines' to comprise cartographically the regional changes in the former distribution of various trees. The complete list of those who contributed to build up our knowledge of the trend of woodland geography and climatic history after the last glaciation in our part of the world is much too long to be given even summarily in this lecture.

New Zealand

As already indicated, we need not confine ourselves to Europe in our pollen-analytical excursions into realms of climatic history. We already have a number of samples of pollen statistics from other parts of the world. Let us go, at once, to the antipodes. Let us examine New Zealand. Carl Caldenius has brought home from that country a collection of series of peat samples which I worked at some years ago together with a guest at my institution, Miss Lucy Cranwell, from the Botanical Museum in Auckland. Our diagram chain (Fig. 7) shows, with the first glance at the general structure of the diagrams, a correspondence with those of Europe, which is too striking to be brushed aside as a chance resemblance. Revertence is present also here. So is regional parallelism, and this not only in the mutual relationship of these diagrams. The development of the vegetation in New Zealand, as expressed by them, can well be regarded as a reflexion of that of Europe almost as faithful as, for example, the diagram from Norrland is a reflexion of that of south Sweden. We have the same three chief zones, the same sharp contrast between terminokratic and mediokratic elements. Zone III shows us how in recent times there appeared both the subantarctic beech wood, consisting of various species of *Nothofagus*, and the same grass heaths which now characterize the high-lying tracts of the South Island of New Zealand from which the diagram originates. In the middle zone there dominates completely a pollen group which rapidly suppresses the pollen characteristic of Zone I, then culminates, and finally recedes to a subordinate position in relation to *Nothofagus* and grass. The mediokratic pollen comes from a series of various coniferous trees most of which belong to the genera *Podocarpus*, *Dacrydium* and *Phyllocladus*, which compose the so-called Lowland Rain Forest of New Zealand. This type of wood now characterizes the lower, climatically favoured parts of the temperate region of New Zealand, but formerly it has manifestly been completely dominant even in those tracts where the *Nothofagus* woods of the mountain climate now prevail. Before the phase of *Podocarpus* there was a time with almost nothing but grass plains, registered in Zone I of the pollen diagrams by dominant grass and sedge pollen. There also occur, in Zone I, abundant herbaceous pollens mostly of species belonging to the subalpine mountain meadows. In the face of these pollen diagrams from New Zealand we must be certain that there, as in Europe, after the shrinking away of the last sheet of land ice up to the alpine valley glaciation of

the present time, there occurred, during two different phases, sweeping transformations of the whole geographical character of the plant world, which without the least doubt were determined by considerable climatic changes. Even if the mediokratic pollen flora does not directly register a warm period yet the parallel with Europe is nevertheless unmistakable.

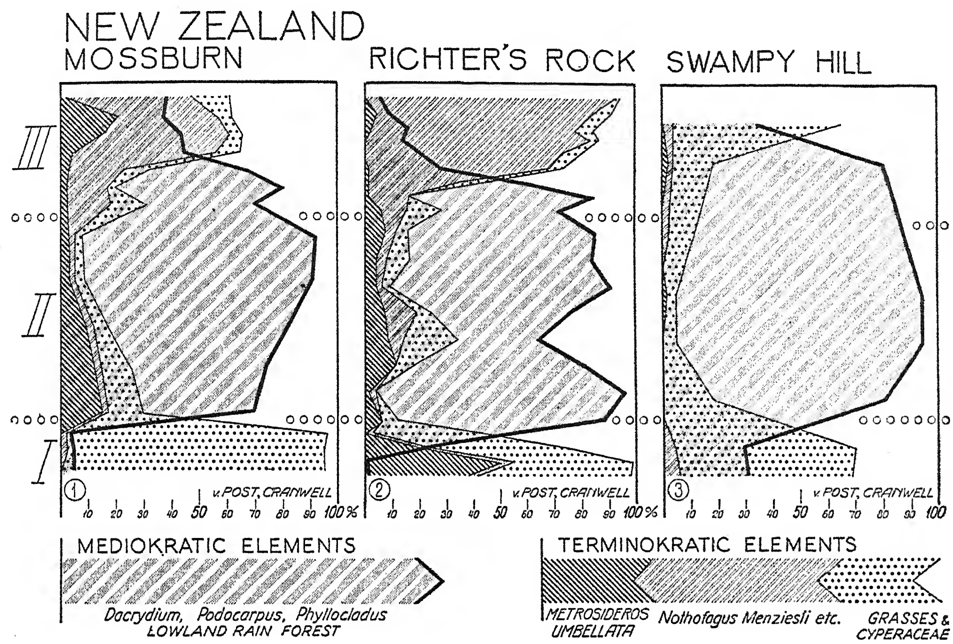


Fig. 7. Synchronized pollen diagram chain from the southern part of the South Island of New Zealand. Revertence in these New Zealand pollen diagrams is striking, but in part rather complicated. In the Swamp Hill curves for grass and sedge, and also, though only feebly, in the *Nothofagus* frequencies, it is unequivocal. In both the other diagrams *Nothofagus* wood in Zone III has replaced the grassland from Zone I. But, as a link between these terminokratic chief elements, there occurs *Metrosideros umbellata*, a forest tree belonging to the Myrtaceae. Both in these diagrams and in three other ones, which were worked out from the South Island of New Zealand, this species reaches its peak sometimes in Zone I, sometimes in Zone III; but it occurs also regularly in varying abundance together with the mediokratic elements of the region, the coniferous wood of the rain forest type, in Zone II.

America

Thanks to the energy of Caldenius as a collector I have also had an opportunity of going through series of samples from post-glacial peat bogs in the southernmost part of South America. My diagram chain (Fig. 8) cuts through the southern half of Terra del Fuego from south-west to north-east, or from Lago Fagnano up in the belt of deciduous *Nothofagus* wood close below to the alpine heath of the east side of the Andes and out into the grass steppe which clothes the lowland towards the Atlantic.* Again we see the same thing...but the mediokratic elements are now grasses and other steppe plants. The north-eastern lowland steppe of Terra del Fuego once reached far up into the present

* A very comprehensive material from Terra del Fuego and Patagonia has also been brought home and published by Väinö Auer and Matti Salmi. This material will, when recast, give a very complete picture of the regional displacements of these parts of South America, even including the west side of the Cordilleras with its evergreen rain forest.

region of woodland. Thus the recession of the steppe is explained, according to my interpretation, most simply and best, by assuming a general decrease of warmth which mitigated the aridity in the rain shadow of the lee side of the Cordilleras. A post-glacial warm period is, in such a case, almost still more strongly indicated in Terra del Fuego than in Europe.

In North America various investigators have carried out pollen analytical work, but the results are as yet in their early stages. We know, however, thanks first and foremost to

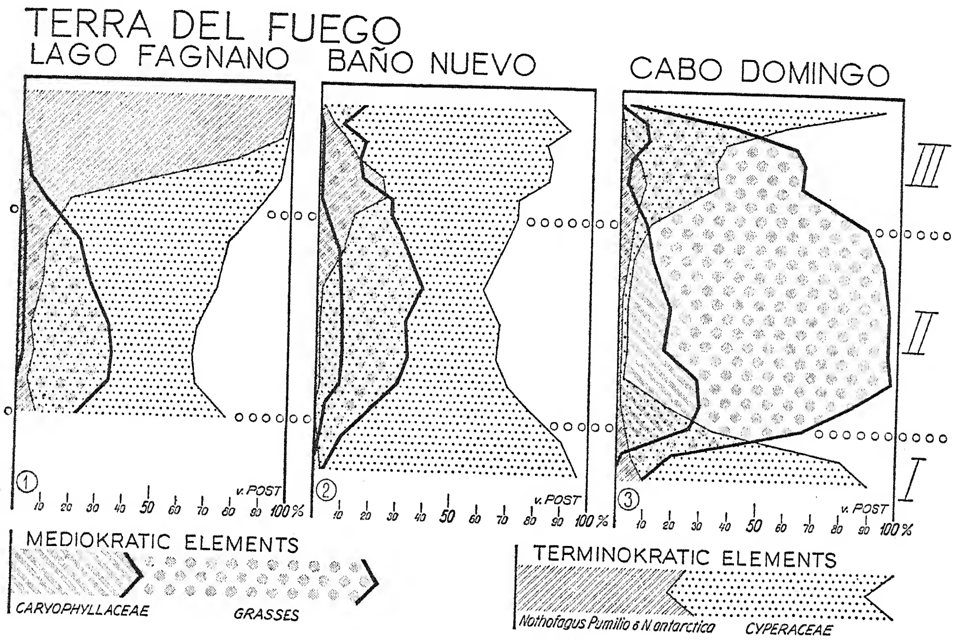


Fig. 8. Synchronized pollen diagram chain from Terra del Fuego. Besides the revertence which is in special evidence in the curve for the Cyperaceae, this diagram gives, in two respects, beautiful examples of regional parallelism. One is the successively diminishing amount of the mediokratic steppe elements from Cabo Domingo to Lago Fagnano. This takes place in accordance with the increasing topographical predisposition to humid climatic conditions. The other is the analogous appearance of *Nothofagus* wood over the arid region in Zone III. We must, however, from the occurrence of the *Nothofagus* pollen, infer a general peak in the humidity at the beginning of Zone I. *Nothofagus*, even the lofty forest tree *N. pumilio*, then extended into the lowlands actually beyond the present boundary of the scattered *N. antarctica* brushwood. *N. pumilio* shows a corresponding peak period even in the actual 'beech wood' round Lago Fagnano, according to the statistics of the number of pollen pores. We must ask ourselves whether Terra del Fuego did not have a subatlantic fimbul winter like the one described by Sernander in Europe. The curves have been smoothed by taking the average of successive groups of the analyses figures 1–5, 2–6, etc. The zone boundaries appear therefore less distinct than in the original diagrams.

Paul B. Sear's material from the eastern United States and Auer's from south-east Canada, that there occurred in the eastern parts of the continent after the last glaciation large phytogeographical displacements. At the University of Stockholm, Carl-Gösta Wenner, in his investigations of north-eastern Labrador, confirmed that these regional displacements extended right out on to the arctic tundra. The results from North America imply that, just as in Europe, the southern woodland elements, e.g. species of oak and hickory in the south, and certain conifers, including species of *Pinus*, *Abies* and *Tsuga*, in the north, were formerly commoner both regionally and quantitatively, but that towards

the present period there has been an expansion of the elements of the north, chiefly various species of spruce, but also of more damp-loving types, such as maples, beeches and swamp trees like *Nyssa* and *Liquidambar*. Sears emphasizes particularly that his pollen diagrams, just as those of Europe, can without difficulty be divided into three chief zones: the lowermost an introductory zone of the warm period, above that a phase of rising temperature and culminating drought, and above that again a stage with progressive cooling and increasing humidity.

Olof H. Selling, at the University of Stockholm, has found on the volcanoes at Hawaii an exactly corresponding system of three periods: first a period with subalpine woodland down to levels below where they now prevail, after that a migration upwards and a general increase of the montane rain forest, which now clothes the lower slopes of the mountains, and finally a depression of all the vegetation boundaries in the direction towards their position just after the ice age.

China

Finally, let us compass another quarter of the globe and visit China. We have, as yet, no pollen diagrams from China, but J. G. Andersson, also a Vega medallist, has found in the peat bogs and layers of prehistoric culture in the climatically inclement plains around Huang Ho, remnants of water buffaloes, water stags, bamboo rats and other types of animals which now belong to the mild regions of Yangtse-kiang, and from a neolithic site of north China, situated in a tract where it is now too dry for rice cultivation, he has brought home pottery bearing impressions of rice husks. The northern boundary of rice cultivation now lies about five degrees farther south. Andersson emphasizes that in China 'the ubiquitous intense cultivation lies like a curtain of smoke over the alterations of nature determined by climatic changes', and that it may be difficult to distinguish the effects of these two factors. All the same he stressed as his personal opinion that certain of his discoveries nevertheless 'seem to bear evidence that it, in fact, is a question of climatic change' (*Ymer*, 1943, p. 90), and in this we can certainly agree with him.

The quaternary ice ages and warm periods

One would hardly exaggerate by saying that we already have indications enough to allow us to venture to speak of an epoch between the last glaciation and our time, during which the climate of all parts of the earth was different from that at present prevailing. On the other hand, however, we have at present scarcely the right to postulate that this epoch was everywhere a period of warmth, even if there is much that supports this view. But one thing we may certainly be sure about; this world-wide wave of climate ranked, in strength and length, with the alterations in the earth's regime of warmth, which, during earlier phases of the quaternary period, resulted in changes between ice ages and interglacial periods.

Albrecht Penck, our Vega medallist of 1923, adopts, in his classical scheme for the quaternary glaciations of the Alps, four ice ages and three interglacial periods. He reckons that between the periods of glaciation the snow boundary in the Alps lay about 300 m. higher than now, and he assumes a correspondingly higher temperature level. The quaternary glaciations were world-wide, inasmuch as we have found their traces in nearly all the regions of the earth where land ice is capable of being formed. And besides this we find other expressions of cooler climate, e.g. the former enormous pluvial lakes in tracts of America, Africa and Asia, which are now desert. From north Europe we know of

parallels to the three last of Penck's alpine glaciations, and thanks to the pollen statistics worked out by Danish, Polish and Russian investigators, from interglacial peat bogs, we are clear about the chief features of forest evolution during the two last interglacial periods.

The diagram chain in Fig. 9 is entirely from Denmark. It thus stretches over no woodland regions in the geographical sense, but it extends through a space of time which probably measures some hundreds of thousands of years. The three diagrams were all worked out by Prof. Knud Jessen in Copenhagen. The one on the right, from north-east Zealand, represents post-glacial time, both the others, from tracts between Ringkøbing and Fredericia in Jutland, represent the two interglacial periods from which peat bogs are found preserved in Denmark. Again we are faced with a correspondence so manifest that

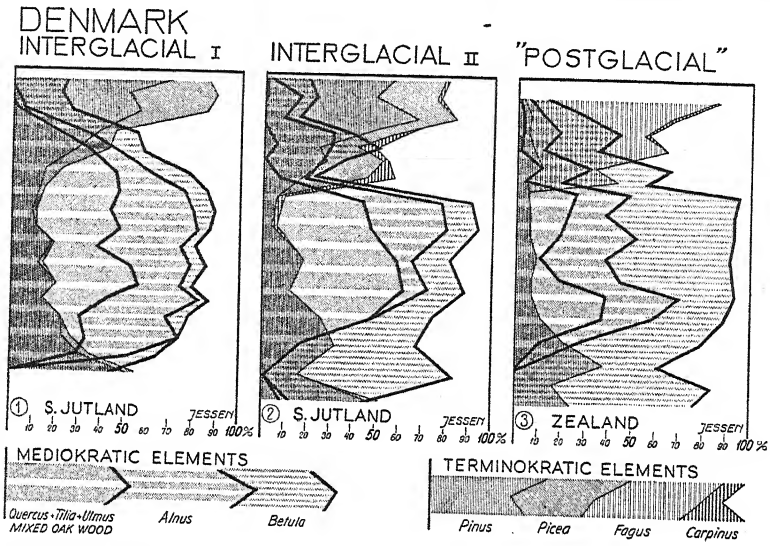


Fig. 9. Pollen diagrams of peat bogs formed between and after the three last quaternary ice ages. The interglacial diagrams are put together according to Knud Jessen's original diagram (*Danm. Geol. Unders.* II R. Nr. 48); interglacial I from Hareskov and Starup, interglacial II from Solsø, Duedam and Rodebæk III. In the other diagrams from interglacial II the Carpinus frequency rises to 60%. In both interglacial diagrams the peat moss sequence is both overlaid and underlaid by alluvial deposits of clay and sand with arctic plant remains. The post-glacial series of layers also rests on strata of this kind.

I need not disentangle the single features, but there are differences too. In the post-glacial diagram it is the beech which replaces the mixed oak wood and alder wood of the warm period. In both the interglacial periods beech is entirely absent, but its satellite, hornbeam, is found in the second interglacial period in considerably more abundance than at any time in the post-glacial diagrams from these tracts. In both interglacial diagrams the characteristics of the more recent phases of development are partly that the spruce rises to high frequency, and partly the returning pine. The spruce is altogether absent from the post-glacial pollen diagrams of Denmark and the pine never reasserts itself in them after its recession during the warm period, but the interglacial diagrams, even because of their pine curves, achieve revertence which is almost absent in the post-glacial diagrams of Denmark. Actually the interglacial development is still more markedly revertent than our examples show, for it both begins and ends with stages in which arctic plant and animal remains are distinctive features. The essential difference from the so-called post-glacial is that the arctic end phase of the latter has hitherto failed to appear. But we can

scarcely repress the thought that the whole course of development points towards such a phase and that what we call post-glacial may be actually an interglacial. It is far from improbable that we have been, for the last 4000 years, travelling towards a new ice age from which we are, however, still separated by an unknown number of thousands of years.

Meiotherm and pleiotherm epochs

But now whether Penck's alpine Würm ice age, the 'Baltic' glaciation of north Europe, should rightly be called 'the last' or 'the latest' quaternary ice age, we are at least certain of one fact: the million years of the quaternary period are, taken as a whole, an exceptional phase within the half milliard of years, of which we know, through fossil faunas and floras, at least the chief features in the history of climate. The little episode in the history of our planet when man appeared and became the ruling animal belongs to what William Ramsay called a meiotherm period, that is to say, literally interpreted, a period with less warmth than that prevailing in the pleiotherm periods which occupy the greater parts of the past history of the globe. To such an epoch with more warmth, again to translate literally, belonged the cretaceous period and the first half of the tertiary period. There then grew at Spitsbergen and Greenland tree ferns, the bread fruit tree, cinnamon, magnolias, laurel, bananas, and similar subtropical plants. This was known for more than half a century from the discoveries made by two of our first Swedish Vega medallists, Adolf Erik Nordenskiöld and A. G. Nathorst, and since that time similar fossil floras have been discovered at high latitudes around the earth. Even before this particular warm period, pleiotherm periods, when the earth's climatic zonation, as in the cretaceous period, seems to have been very nearly smoothed out, alternated with meiotherm epochs during which glaciation occurred in the extreme periods. The wave length of these cycles appears to be of the order of magnitude of 200–250 million years. The quaternary period marks the bottom of a trough in this large swing between pleiotherm and meiotherm. It is, taken as a whole, an epoch of glaciation, the third of those of which we have certain knowledge in the history of the earth. Like its predecessors the quaternary glaciation epoch is divided into the cooler or milder climate phases, which we call ice ages and interglacial warm periods, but fluctuations like these are only ripples on the immense wave of cold, however gigantic they may appear when measured by the human scale. As far back in time as to these ripples, stretch the chapters in the palaeoclimatic annals, the key to whose cypher pollen analysis has proved to be, but the geohistorical climatic changes of a still higher order lie, for the present, outside the bounds of this method. Attempts have been made with pollen statistics for tertiary and even older prequaternary series of beds, and these experiments actually show promise. They have, however, not got beyond the first stage of groping.

Minor palaeoclimatic fluctuations

You are wondering about these 'ripples'. At the beginning of this lecture it was mentioned that the curve for the fading out post-glacial warm period undulated with a series of alternating warmer and colder phases in correspondence with the recurrence surfaces of Granlund. Have the pollen diagrams nothing to say about this? Indeed they have, but the diagrams which are shown have been chosen, or have been treated, in such a way that details of this kind might disturb the general picture as little as possible. Nevertheless there are, even in these simplified diagrams, various minor features in the course of the

curves, which recur with such consistency that they can be scarcely dismissed as simply accidental. Look, for example, at the sudden movements affecting both birch and pine during stage I in nearly all the Swedish and west European diagrams (Figs. 5, 6)! And look at the pair of diagrams from Sollefteå and Junosuando in Fig. 5. It becomes still more apparent, by looking at these diagrams in their full details (Fig. 10), that small

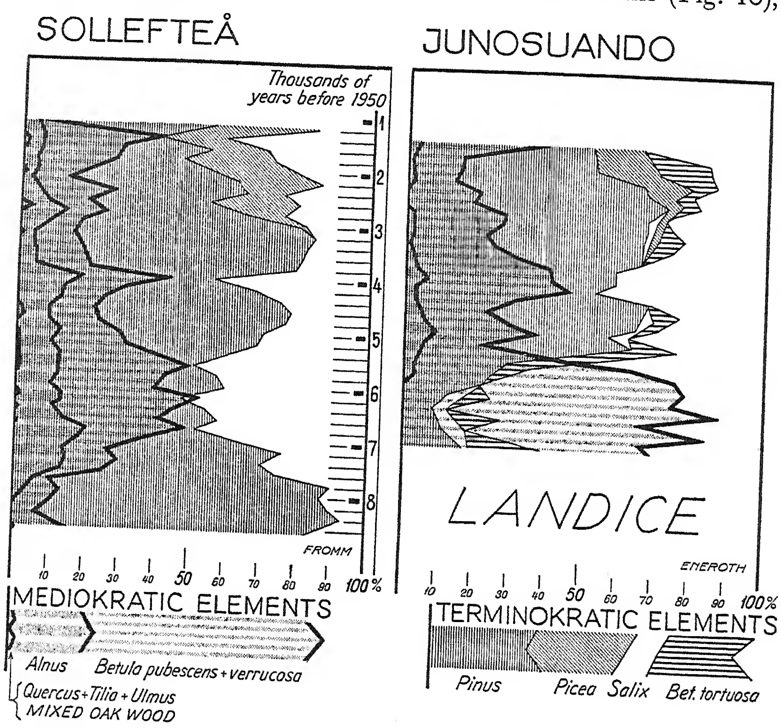


Fig. 10. Synchronized pollen diagrams of sediments of a former fjord of the Ångermann River (Sollefteå) and a bog in north-east Lapland (Junosuando). The diagrams demonstrate that even minor variations in the composition of the pollen flora may recur regionally, and consequently be of essential bearing. In this pair of diagrams the pollen spectra have been extracted from the original diagrams with distances half as great as the corresponding ones in diagram chain Fig. 5, i.e. for every 200 years at Sollefteå. The amazingly accurate conformity between the total curves of the mediokratic elements, or, as the case may be, terminokratic elements, in both diagrams came to light owing to Prof. Eneroth's 'birch analyses' in his Lapland diagrams, of which that from Junosuando is one, and which all show very strong mutual resemblance in the details. In these Laponian diagrams we have to exclude *Betula nana* and to transfer *B. tortuosa* to the terminokrata in order to obtain a rational distribution of the pollen flora in its two main groups. Among the birch pollen of the Sollefteå diagram neither *B. nana* nor *B. tortuosa* can be expected to occur. In the lower portions of the Junosuando diagram *B. tortuosa*, in the final drawing, has become somewhat too broad at the cost of the willows.

variations can also reflect details of development of such regional extent that we must unquestioningly interpret them as climatic effects. In spite of the distance, very nearly 600 km., the conditions change between mediokratic and terminokratic in a rhythm nearly identical and, besides that, rather complicated.

Finally, one more pollen diagram, the last that I shall show this evening (Fig. 11): it is from Snöromsmossen in Nacka near Stockholm, known as one of the chief localities of Granlund's investigation of the recurrence surfaces and their dating. It was worked out in 1934 at the Geological Institute of Stockholm University by the Norwegian pollen

analyst Asbjörn Ording, and stretches from about Granlund's RY III, i.e. Sernander's post-glacial climatic deterioration, up to the present time. The diagram has only 2 cm. between the levels of analysis, against Granlund's 5. It therefore shows the course of the curves considerably more exactly than that published by Granlund (S.G.U., Ser. C, No. 373, p. 82). The diagram struck Ording and me by its obviously rhythmic birch curve and just as obvious connexion between the fluctuations of the birch curve and the recurrence surfaces. As to the latter Ording found that Granlund, like Sernander with his four-period system, had discovered only a part of the truth. Ording showed, by means of a special method of his own, that also in Snöromsmossen the absolute pollen amount

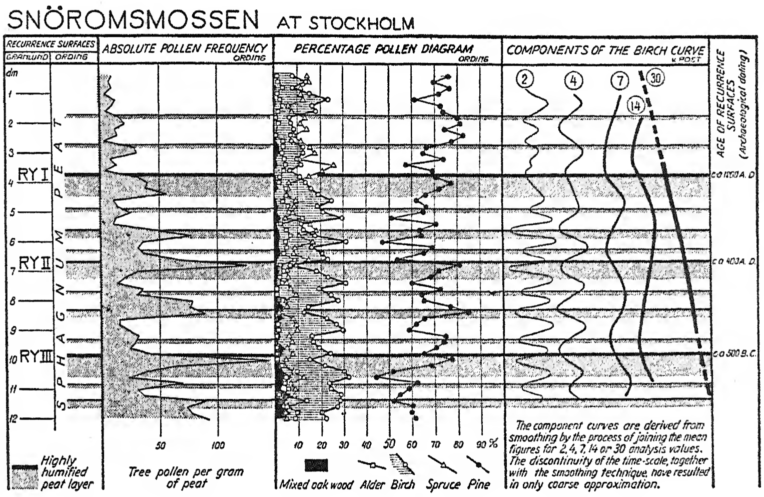


Fig. 11. An attempted analysis of the complex periodicity which is sometimes to be discerned in the course of the curves of the pollen diagram. Snöromsmossen became a classical example through Erik Granlund's description of its recurrence surfaces. Its pollen diagram is related to the north Swedish type by the dominance of the birch among the mediokratic elements. The curve for Ording's pollen frequency reflects, as do the changes in the degree of humification of the peat, variations in the intensity of peat formation from time to time. High pollen concentration, or highly humified peat, signifies, in a raised bog like Snöromsmossen, slow peat formation, i.e. low water supply and dry climate. Low pollen content and weak humification imply that the layer in question was formed under damp conditions which hastened the deposition of peat. The birch curve is regularly connected with Ording's perfected system of recurrence surfaces in such a manner that the birch maxima, i.e. the phases when the climate was more maritime, correspond to layers of peat formed under more humid conditions. The component curves show us, through Granlund's dating of some of the recurrence surfaces, approximate period lengths of about 1700 years, 800–900 years, and about 400 or 200 years for the undulations of the climate.

regularly rose and sank with the higher or lower degree of humification of the peat. The larger concentration of tree pollen in the more humified layers of peat indicates that during the period when these were formed the growth in height of the bog had been retarded so that the pollen rain from a greater number of years got into the samples analysed than was found in analyses from less humified, more quickly formed sequences of beds. It also appears both through a more thorough investigation of the changes between different degrees of humification and of curves for the absolute pollen number that there are, between the recurrence surfaces described by Granlund, more weakly developed ones. Even these recurrence surfaces of lower order corresponded with marked oscillations in the birch frequency. By smoothing the birch curve I could further

establish that it is composed of five elementary curves, of which four are clearly rhythmic and have successively diminishing wave-lengths. The one with the longest wave-length, of which only a fraction is present in the series of beds analysed, shows the ordinary diminution of woodland birch of the warm period towards the present day. But the relationship of the four remaining ones towards each other and towards the system of recurrence surfaces is highly remarkable. In both the most strongly developed recurrence surfaces, Granlund's RY III and Granlund's RY I, all the component curves of the birch pollen sink; in the next most marked one, Granlund's RY II, three of these curves sink; and in both the weaker recurrence surfaces, which Ording discerned, two, or only one, of the birch curves sink. That we are not dealing with a mathematical fiction seems to me proved by the correlation with the recurrence surfaces. We have here found the climatic changes of the last 2500 years registered consonantly by two reactions wholely independent of each other, i.e. in the deposition of peat in Snöromsmossen and in the relative frequency of birch in the Nacka woods.

It is an extensive undertaking to unravel thoroughly the complex of problems which Ording's diagram from Snöromsmossen puts before us. Time and people have been lacking. This much, however, is made clear by this diagram and by many other observations: the detailed course of the climatic changes has been exceedingly complicated, but beyond the intricate picture we catch a glimpse of a mathematical law which perhaps will ultimately appear quite simple. Definite pointers in this direction had already come to light before Granlund introduced the concept of recurrence surfaces, and it was with these things, among others, before my eyes, at the Botanical Congress at Cambridge in 1930, that I proposed to change Sernander's classical four-period system to the three-period system, which we saw appearing in the diagram chains from one part of the world after another. I suggested this system only as a provisional measure anticipating the final chronologically constructed system which may include the complete course of development in all its kaleidoscopic synthesis of larger and smaller climate waves. To fix this system is one of the most important tasks of the future. It should be realized all round the world, but this must be done without bias, and independently within each of the various areas of work. For following a stereotyped plan leads here, as always, into a blind alley, and it is not to be expected that the course of the climate curve has been the same in detail in all parts of the world, though in its main features it shows such a striking correspondence.

Theories

In what I have said I have hesitated in my speech, when dealing with the nature of climatic changes, in such a manner as to astonish my audience, and about the causes, which are, nevertheless, the kernel of the problem, I have kept silent. Both these things I have done intentionally. For it might be indisputable that there was a wave of warmth in Europe, which determined the general course of post-glacial development. Very likely this has in fact been the case in North America and Terra del Fuego, but in the South Island of New Zealand and in China it is only more copious precipitation that is clearly indicated. About the driving force at the back of the climatic fluctuations of higher and lower order, which we may define or surmise, we still stumble in deep ignorance, in spite of all speculations about it.

Many attempts to explain the quaternary change between ice ages and warm periods

assume that the poles and parallels of latitude have altered their position, but such theories are denied by the ever increasing proofs that the ice ages were synchronous in all parts of the globe, and we feel ourselves justified in applying the pointed remark of Sir Albert Seward, the great English palaeobotanist, when speaking of the cretaceous and tertiary subtropical vegetation in the polar lands: 'Whatever the solution may be, it is hardly likely to be found by taking liberties with the North Pole.' William Ramsay's relief hypothesis can possibly explain the occurrence of glacial epochs as extremes in the vacillation between pleiotherm and meiotherm periods, but it has nothing to say about the phenomenon of ice ages and warm periods within the glacial epochs, for there is scarcely any rhythm in the formation of mountain chains which could correspond to the swelling and shrinking of the quaternary land ice. For these phases in the palaeoclimatic chain of events, explanations, based on astronomical calculations, have been proposed by Milutin Milankovitch, Professor of Celestial Mechanics at Belgrade University, and also by the climate expert W. Köppen: Sir George Simpson, the former head of the meteorological department in England, has also put forward a theory of the ice age with long period variations in solar radiation as a basis. But 'grau ist alle Theorie', especially when, as in this case, attempts are made to fit a course of development into a chronological system which is borrowed from a range of outside phenomena. If the facts appear to agree approximately then the theory becomes positively dangerous, for it may tempt us to wishful thinking which obscures our vision of the empirical realities. This has happened to a lamentable extent in dealing with the quaternary climatic history. We must, of course, at first define objectively the courses of events that are to be explained, and neither for the post-glacial climate development nor for the climatic revolutions of the older quaternary phases have we yet got the basis for a sound interpretation.

Registration of climate by the ocean surface

Thus, for the present, it is upon the course of events that the exploration of the earth's climatic history must concentrate. For the time after the latest ice age the palaeoclimatologist has two roads open. The one, a short cut, goes via the changes in water-level of the ocean. Dependent upon the amount of the world's total water supply lying stored up in land ice, the ocean basins have been filled to a varying height. It has been calculated, on very uncertain data, that the surface of the ocean, during the latest general glaciation, stood about 75 m. lower than its present level. At all events the restitution to the ocean of the quantity of water that lay stored up on the continents during the Würm period has brought about a raising of the ocean surface of several tens of metres, although this so-called eustatic heightening of the ocean may not have progressed uniformly throughout the ages. It must have been hastened, slowed down, stopped, or perhaps reversed into temporary sinking, as the formation or melting of land ice had the upper hand quantitatively. As an example we may take the curve of the displacement of the sea beach at Göteborg during one of the waves of transgression, into which the large eustatic rise after the ice age was divided (Fig. 12).

A perfect curve of the changes in height of the ocean surface throughout the post-glacial period will give a collective expression of the changes in balance between the formation and melting of land ice over the globe. To plot this curve for the complete period after the latest ice age is the chief aim in the unravelling of the marine beach

displacements of the former fjord of the present valley of River Viskan, which the Geological Institute of Stockholm University carried out during ten summers, and the field work of which was completed in 1943. It can be promised with certainty that, when the working up of the material of the Viskan investigations is completed, as it will be in a few years, such a curve will be presented. By this curve we shall have obtained a picture of the collective effects of climatic changes in the world during the late quaternary period and, what is still more important, a means will be obtained, as precise as can for the present be expected, of determining the time relationship, without subjective speculations, between those changes of climate which in other ways could be reconstructed within various regions of investigation round the world, for the eustatic curve is indeed one and the same over all the seven seas. If we succeed, as we have at River Viskan, in linking

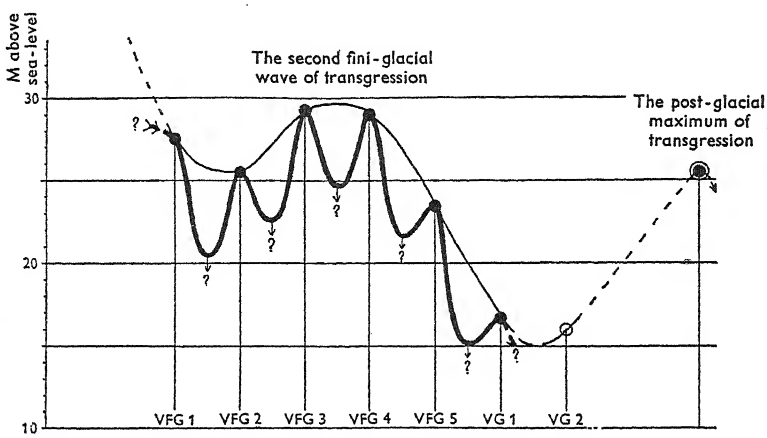


Fig. 12. A portion of the curve of the post-glacial beach displacement at Göteborg. The displacements of the sea beach after the ice age are, in Fennoskandia, the combined effects of two factors independent of each other: on the one side raising of the land, and, on the other, the absolute alteration in level of the sea. If the raising of the land is sufficiently weak we get the course of development which can be read off from a series of raised beaches of different heights dominated in its details by the eustatic changes in water-level of the ocean. These changes are, as explicated in more detail in the text (pp. 213 f.), the collective expression of variations in the total heating mechanism of the world. Various facts have come to light which indicate that, even in these, a complex periodicity was in force. The wave of ascent in the Göteborg curve with its small oscillations corresponding to the individual beach levels is an example of this. The numbers of the raised beaches (VFG 1–VG 2) refer to the beach line system at the Vänern basin.

together the history of vegetation in different parts of the world, registered in pollen diagrams, with the changes in water-level of the ocean, then we can also fit the history of the vegetation into the general chronological system. Unfortunately, there are few regions with such favourable conditions for reconstructing the rising curve of the ocean as Fennoskandia with its land elevation after the ice age and its almost complete freedom from tectonic disturbances of level relationships.

It is the second of the two ways in view that can be expected to lead forward to the supply of knowledge we need in order actually to interpret the post-glacial climatic history of the world in all its principal implications. This way is to investigate a sufficient number of regions, which are methodically dispersed over all the more important climatic provinces of the world. By comparing the results from these regions we should be able to draw definite conclusions from what appears to have happened in particular regions and about what actually happened with the whole.

THE POST-GLACIAL CHANGES IN THE WORLD'S SYSTEM OF CIRCULATION

It is by no means difficult to find a fairly satisfactory explanation of the post-glacial warm period in Europe. The Gulf Stream is the great heating system of our part of the world, and it extends its effects as far as Russia. Nothing more is necessary than changes in strength and heating power of the Gulf Stream to explain both the European warm period as a whole and the minor oscillations between continental and maritime conditions, such as are indicated by Granlund's recurrence surfaces in the bogs. It is just as easy to seek an explanation for the former expansion of the *Podocarpus* forest in New Zealand, by means of the stream complex around the South Island. In both these regions it is, of course, ultimately the changed pressure of the air and winds which turn the scales. In eastern North America it might be a strengthening of the North Atlantic summer high pressure that brings about increased supply of warm air from the south. In north China it is the south-east monsoon which is apparently responsible for the increased supply of water that made rice cultivation possible, and in Hawaii we have the north-east trade winds to manoeuvre with. Finally, in Terra del Fuego, the affair is either, as Auer supposes, exceedingly complicated, or else so simple that it is merely a question of a direct warmth reaction. Now we have seen that all these entirely different climatic fluctuations took place in one and the same rhythm in whatever part of the earth we meet them and whatever their immediate cause may be supposed to have been. We have, then, to inquire for a common, fundamental cause, for a factor which swayed the planetary circulation system of the ocean as well as of the air, so that the different reactions we can trace are synchronously released in all the individual 'organs'. If we wish to find this factor, we must, of course, make the circulation machinery as a whole the object of our investigation.

It goes without saying that we must, with our system of observations, cover not merely hemispheres and quadrants, but every main division of the earth's circulation system. We must not relax our efforts until we have found out the climatic historical course of development in the cyclone belts as well as in the regions of the trade winds of both hemispheres, and in the equatorial zones. Where opportunity offers, e.g. in New Zealand, in east Asia and Pacific North America, the continued investigation should be directed to determining the latitudinal displacements in the same way as this has been done in Europe and in eastern North America, but it is also important, particularly in the tropics, to select districts for investigation so that we obtain the measure of climatic changes in the form of figures for the vertical zone displacements within suitable mountain tracts. The map (Fig. 13) shows a first sketch for a plan of the system of districts to be investigated as I now conceive it, but I shall not enter into details, for the system will certainly need to be both modified and completed when the work is properly started.

The final unravelling of the earth's post-glacial climatic history will throw light not merely on the ages immediately concerned, but also on the complex of problems of the quaternary climatic variations in their entire extent. We have seen how clearly post-glacial climatic development ranges itself into the rhythmic changes between ice ages and warm periods. When once the secret of the cause of the post-glacial waves of climate is exposed, then the riddle of the quaternary ice ages will no doubt be solved.

It is axiomatic that such considerable revolutions in the very heart of natural conditions,

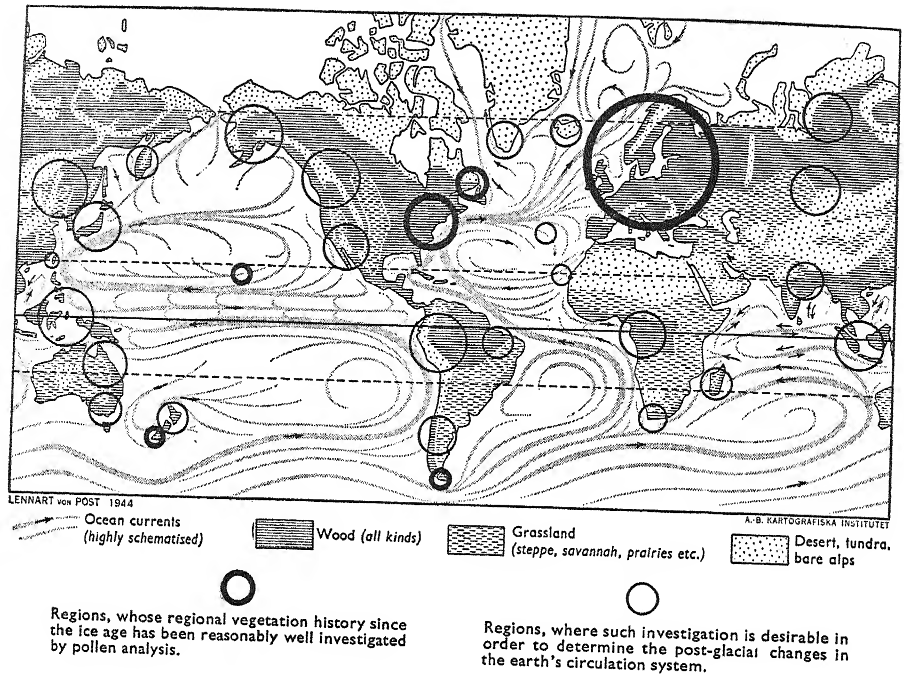


Fig. 13. A preliminary sketch for a scheme of systematic investigation of the post-glacial changes in the earth's circulation system. The investigations by pollen statistics in different parts of the world have shown clearly that, after the latest ice age, world-wide climatic changes took place, which everywhere, in the main, followed the same rhythm, and which in order of magnitude can be compared with the quaternary oscillations between ice ages and interglacial warm periods. Within each of the areas the post-glacial climatic changes can, without much hesitation, be referred to changes in the circulation of air and water in the region in question, but then we are faced with the fundamental problem of determining these changes of the circulation system in their entirety in order to circumscribe their fundamental cause. Regional elucidation of the history of the vegetation, by means of pollen diagrams, and reconstruction of the former watering conditions, by investigating peat bogs and former lakes, etc., have been found to be effective means of attaining palaeoclimatic knowledge of epochs after the ice age. With these methods of investigation, used within methodically chosen areas around the world, we should be able eventually to solve the problem of the post-glacial climatic changes. The start towards this goal is made. Besides the fairly advanced investigations in the countries here treated, more or less energetic and successful advances have been attempted in, for example, north-west America (Osvald), Kamtschatka (Erdtman and Hultén), Siberia (Gerasimow and others), Iceland (Thorarinsson) and Greenland (Iversen), but the greatest part of the work remains to be done, even within the regions mentioned. Within the cyclone belt of the northern hemisphere two sets of investigations must be carried out. First, in order to get a grasp of the air pressure centres over the North Atlantic, we need as full details as possible from the Azores, Iceland, Greenland and Florida. Secondly, in order to obtain the changes in effect of the Kuroschio and California current, we need regionally exhaustive investigations in the north Pacific coast of east Asia and North America. These investigations should be extended from the polar woodland limit as far down as possible into the subtropical regions. In addition to this attention must be paid to the changes in strength of the continental anticyclones in north Asia and North America, preferably by investigating the interiors of the continents. The vertical displacements in the system of regions must also be exactly determined. Within the cyclone belt of the southern hemisphere the pollen diagram system from Terra del Fuego, Patagonia, and the South Island of New Zealand should be extended as far as possible to the north along the Andes and on the North Island of New Zealand, and preferably also Tasmania, the Australian Alps and the Cape should be investigated. In the trade-wind regions Madagascar and the north-west African volcanic islands seem to be of primary importance for the completion of the results from Hawaii and the African-Indian monsoon region, and for example certain tracts in the south-eastern Himalayas or south China. North-east Africa (including Abyssinia) has already been found unsuitable for investigations of this kind. Finally, within the equatorial belt, data are first and foremost desirable from Indonesia, from the Congo basin with its marginal mountains, and also from the Andes in Ecuador (including Colombia and northern Peru) and the abutting regions of rain forest in the Amazon basin. It is of primary importance, in

which we find registered in pollen diagrams from different parts of the world, must have set their trace on mankind's destiny from the disappearance of the very latest land ice and right on till material culture reached stages in which people could, at any rate in some measure, become independent of natural conditions of life. But until this took place, both the changes in climate themselves and their geographical results must often have brought about weal or woe for considerable groups of mankind. Particularly at the limits of human cultivation, such as Greenland or Iceland, or the extensive plains in Asia, Africa and America, which hovered between, on the one side, the barrenness of a desert, and on the other, the more or less good pastures and possibilities of cultivation in the grass steppes and forest land, it is inconceivable that changes in the natural conditions should not have had sweeping results on both the distribution and standards of living of mankind. Certainly cultural, social, political and folk-psychological factors have many times been the driving force both of migrations of peoples or of the flowering or fading of former cultures. None the less the conclusion seems inescapable that changes in natural factors must be considered if we wish to reach a true understanding of these phenomena, indeed that these changes may have occasionally been fundamental. In dealing with the problems of cultural history the reconstruction of the history of nature should be considered a necessity.

The work can be carried out, thanks to the scientific methods and the definition of the problems to be solved in detail, which grew up in Sweden during the 50 years after Rutger Sernander opened the field of work which deals with post-glacial history of climate. The investigations should be concerned not only with the structure of peat bogs, but also the further course registered in the history of the vegetation in pollen diagrams. Where peat bogs are not found, depositions of silt in inland lakes and rivers might be examined, but in extremely arid regions this road seems barred to us, for, according to the experience of Erik Nilsson in dealing with the glacial lakes of eastern equatorial Africa, everything organic which manifestly has been present in the now desiccated sediments of the former lakes has become disintegrated by the intensive weathering of later dry periods.

A plan of work of the extent here sketched can scarcely be carried out without organized international collaboration. At the head of this must stand a scientist with experience, foresight, mental acuity and activity, and he must be young, for the task is a life's work.

No one of my generation may live to see the day when even the post-glacial key chapter of the earth's quaternary climatic history will be written and interpreted, but it is my lively hope that the Swedish Society of Anthropology and Geography will obtain chances of supporting, and in due season rewarding, this achievement. That Vega medal will be well deserved.

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these areas, to follow the regional displacements in mountain chains and alpine summits. It is desirable, on the whole, to obtain material for a profile of the vertical regional displacements after the ice age throughout the Western American Cordilleras from Terra del Fuego to Alaska in order to be able to make a comparison with Fritz Klute's conclusions about the lowering of the snow boundary during the ice ages in this and other areas. As soon as times allow an international organization for palaeoclimatic research should be formed. This organization should at first concentrate on post-glacial climatic history but later it could take up, as well, the older quaternary phases and the pre-quaternary ages with a view to determining the character of climates and their distribution in the world.

Stockholms Högskolas Geologiska Institut
February 1944

THE MICROBIOLOGY OF ACID SOILS

I. 'MOR' BEARING *PINUS SYLVESTRIS* AND *BETULA PUBESCENS*

By J. G. BOSWELL and D. J. GOVER

The University, Sheffield

This is the first of a series of publications on the chemical constitution and microbiology of acid soils in the neighbourhood of Sheffield. Other papers will deal not only with general microbiological problems of these soils but also with the metabolic activity in pure culture of some of the organisms isolated.

Location and vegetation

The soil was obtained from a small wood at Ringinglow, 350 m. above sea-level, on the eastern slope of the moor which, stretching westward from this point to the Derwent valley, reaches a maximum height of 450 m.

The tree cover consists of *Pinus sylvestris* with *Betula pubescens*, and the field layer is dominated by *Deschampsia flexuosa* with *Galium saxatile* also present. Over considerable areas *Deschampsia* is the only plant present, and its roots form a thick mat some 5 cm. thick overlying a dark brown humus layer in which partially decayed plant remains are clearly visible. This humus layer is 8–10 cm. in depth and the organic matter is mixed with sand from the under-lying layer. The soil used in the microbiological investigation was removed from this layer, each sample extending from the top to the bottom of the layer and being thoroughly mixed before use. Sharply divided from this layer is the underlying sandy zone, light brown in colour and granular in appearance and about 14 cm. deep. The content of organic matter in this zone is small and decreases rapidly with increasing depth. Samples from this layer were examined solely from the chemical aspect.

Chemical analyses

Table 1 gives information about the soil layers, the upper being the humus zone, the middle and lower forming the underlying sandy zone. The upper layer was examined in greater detail, and the values recorded in Table 2 are from 100 g. organic matter.

The total acidity of one sample of the upper layer was 97·8 m.equiv./100 g. dry wt., of which 22·8 m.equiv. were from substances removable by successive extraction with benzene, alcohol and water. 18·2 m.equiv. were from substances insoluble in these solvents but soluble in 1 % NaOH cold; the residual 56·8 m.equiv. were due to substances in the ligno-cellulose complex, since it was clear that the residual inorganic matter contributed nothing to the acidity of this fraction. Using the ether-extraction technique on soil acidified with $2N\,H_2SO_4$ to about pH 1, the total ether-extractable acidity was 6·1 m.equiv./100 g. dry wt. This may be regarded as the acidity due to a well-recognized group of biologically important organic acids, and of the total 0·9 m.equiv. was due to 'oxalic acid'.

The titration curves showed that the soil contained both weak acids and bases; the almost straight-line form of the curves between *p*H 10 and 4 suggested that a number of acids and bases contributed.

E_5 for undisturbed samples over the period May–September 1943 showed little variation from the average value of 423 mV. Nitrate was never present. E_5 is the estimated potential at *p*H 5, obtained by increasing the observed value by 58 mV. for every decrease in *p*H of one unit.

Table 1

	Upper	Middle	Lower
Depth below root layer (cm.)	0–10	10–17	17–24
*p*H	3·28	3·10	3·30
Moisture content (%)	64·9	29·8	12·2
Organic content as % dry wt.	56·3	15·2	4·6
Acidity (m.equiv.)/100 g. dry wt.	97·8	28·8	12·2
Acidity (m.equiv.)/100 g. organic matter	174·0	191·0	267·0
Residue following extraction with benzene, alcohol, water and 1 % NaOH			
Acidity (m.equiv.)/100 g. dry wt.	71·3	4·0	0·15
Acidity (m.equiv.)/100 g. organic matter	180·0	35·8	10·0

Table 2

	g.
Soluble in benzene	2·35
Soluble in 95 % alcohol	11·96
Soluble in water	8·62
Soluble in 1 % NaOH, cold	36·20
Cellulose	27·90
Lignin	9·95
	96·98
Total nitrogen	2·50
Amino nitrogen-alcohol soluble	0·01

Microbiology

The values recorded below are per gram of soil in the natural state with regard to water content.

The bacterial counts were made on glucose-peptone agar. Only isolated records were made of the total counts, and it is not possible to give a picture of seasonal changes. The following values from a sample taken on 26 November 1944 indicate the order of magnitude of the number of organisms which grow on this type of plate:

$$326 \times 10^6, \quad 394 \times 10^6, \quad 331 \times 10^6, \quad 338 \times 10^6.$$

While it is recognized that similar counts of fungi have no great significance except possibly in the case of the yeasts, fungal counts were made using 2 % malt agar. The following values were obtained from a sample taken on 12 February 1945 and indicate the order of magnitude of the counts:

$$3{\cdot}04 \times 10^5, \quad 2{\cdot}70 \times 10^5, \quad 3{\cdot}36 \times 10^5,$$

$$3{\cdot}30 \times 10^5, \quad 3{\cdot}12 \times 10^5, \quad 2{\cdot}92 \times 10^5.$$

Of the fungi present yeasts were the most numerous on the malt agar, accounting for between 40 and 70 % of the total colonies; of the remainder *Penicillium* was most abundant.

The most prominent colonies were those of the dark brown *Dematium pullulans* which was always present to the extent of 2–3%, and a *Cephalosporium* species in about the same numbers. Using the medium acidified to *p*H 4 these two fungi became much more abundant. Species of *Mucor*, *Rhizopus*, *Aspergillus*, *Actinomyces* and *Botrytis* rarely developed on plates prepared from soil extracts, but they developed rapidly and showed abundant growth when particles of soil were spread on malt-agar plates followed by incubation at 22° C. It is probable therefore that these fungi were present in soil in an active vegetative form. Microscopic examination of the soil revealed abundant hyphae.

The effect of the constitution of the medium on the growth of the fungi is most clearly shown by the great increase in the number of yeast colonies which occurs when gelatin is added to the malt agar plates to give a concentration of 2%. The number of yeast colonies is approximately doubled on the malt gelatin in comparison with the malt medium.

While the culture media provide evidence of the fungal spores which are present in the soil the extent to which these organisms can multiply at the natural acidity of the soil is suggested by the following results:

*p*H	6·5	5·5	4·5	3·5
No./g. soil	$3{\cdot}26 \times 10^5$	$3{\cdot}08 \times 10^5$	$2{\cdot}12 \times 10^5$	$0{\cdot}8 \times 10^5$
% yeasts	49	29·6	30	0

The failure of yeasts to develop at *p*H 3·5 suggests that they have little part in soil metabolism under natural conditions, although apparently present in considerable numbers. The number present may be due to the existence of colonies in isolated pockets in which owing to the constitution of the neighbouring organic matter the *p*H in the vicinity of the organisms approaches neutrality. The fungi which develop at the lower *p*H values are species of *Penicillium* and *Actinomyces*, in particular the number of the latter which occur is increased and accounts largely for the actual increase in the number of non-yeast fungi which appear at *p*H 5·5. With media at *p*H 2·5 only occasionally did fungal colonies appear, and in all cases these were *Penicillium* spp. The bacteria which develop on the glucose-peptone plates are naturally confined to one physiological group, those which can satisfy their nitrogen requirements by decomposing peptone. A wide range of morphological forms was observed, chiefly rods of variable dimensions and only rarely cocci. Spore formers and non-sporing types were present and among the sporing rods (Bacillaceae) were cells with a pair of polar spores and others with only a single central spore producing cell distension. In some cultures the cells joined to form filaments up to 12 units in length, while in one the cells aggregated into small groups surrounded by mucilage. Metabolically some were obligate and others facultative aerobes. This group of micro-organisms is under more detailed examination.

Cellulose decomposition

Strips of filter paper were partially immersed in a suitable inorganic culture solution and inoculated with a water extract of soil—1 ml. from 10 g. soil in 500 ml. water. After some weeks the submerged cellulose and the medium turned dark brown in colour, the latter developed a well-marked acidity, the cellulose at the air-water interface disintegrated and pink gelatinous masses appeared in the zone of decomposition. A small rod-shaped organism appeared to be the active agent. Little or no decomposition occurred

under anaerobic conditions. It is difficult to determine the importance of this organism in the process of cellulose decomposition in the soil, since its activity in pure culture is greatly depressed by increases in acidity. At *p*H 6·5 it decomposes cellulose actively, at 5·5 less actively, and at 4·5 and below no sign of cellulose decomposition occurred after 1 month. The possibility must be considered that since these organisms only decompose cellulose when in actual contact with the fibres, and since cellulose behaves as a weak acid (Rabinov & Heymann, 1941), it may be that these bacteria exist in a microclimate less acid than the reaction of the whole soil and are therefore more active in the decomposition of the cellulose in the soil than would be estimated from their activity in aqueous media at different *p*H values.

When sheets of filter paper moistened with a suitable culture solution were inoculated with a little soil after 1 week at 25° C., species of *Penicillium* and *Aspergillus* were strongly developed and *Fusarium* had frequently appeared. When the culture medium was adjusted to *p*H values as acid as 3·5, *Trichoderma* sp. developed. *Actinomyces* appeared occasionally, irrespective of the *p*H of the culture solution. Of all the fungi which appeared species of *Aspergillus* produced the most extensive decomposition after culture for 2 weeks.

Protein decomposition

The protein-decomposing organisms isolated from the soil were very active in decomposing a 5% gelatin: 1% peptone medium. The decomposition resulted in the formation of amino acids and, following deamination, of free ammonia and organic acids. Mixed cultures of the organisms were incubated at 30° C. for 1 week with a protein-peptone medium. It was found that the amino acid/organic acid ratio varied between 1·25 and 1·93 with an average value of 1·55. The cultures used were obtained from soil samples taken over a period of 6 months. From the mixed cultures a very active protein-decomposing rod form was isolated which under the same experimental conditions gave the amino acid/organic acid ratio as 1·40 aerobically; under anaerobic conditions the organism was equally active but with a ratio of 1·61.

Sugar fermentation

The inoculation of a 1% sucrose solution contained in Pasteur tubes with mixed culture from a soil suspension resulted in rapid fermentation with the production of acid, gas and alcohol. The alcohol was probably the product of yeast fermentation, since colonies of this fungus appeared on the surface of the solution after a few days. The gas produced consisted in part of CO_2, the percentage varying between 25 and 53, being least in cultures prepared from soil during May and greatest in September.

Nitrifying bacteria

The presence and activity of organisms capable of oxidizing ammonia and nitrite in the absence of organic matter were investigated by the inoculation of suitable media, in some cases with particles of soil and in other cases with soil extracts. With certain soil samples no oxidation of either ammonia or of nitrite occurred, and with one sample nitrite was reduced to ammonia. With a few samples oxidation of the substrates was observed, but this occurred at a very slow rate, and after incubation for 1 week nitrite was present in a concentration of about 10^{-4} and nitrate about 10^{-5} in solutions which initially contained

only ammonia and nitrite respectively. The identity of the organisms was not further investigated, but it is not possible to assume that they were *Nitrosomonas* and *Nitrobacter*, since H. Winogradsky (1935) has noted the existence of certain slow-acting nitrifiers, a nitrite-former, *Nitrospira*, and a nitrate-former, *Bactoderma alba*, and the presence of capsuled or *Nitrocystis* strains in forest soils.

Nitrogen fixation

Two media were employed, one containing mannitol as the sole carbon source and the other containing glucose; the first was used for the culture of aerobic organisms and the second for the culture of anaerobes. Cultures were inoculated either with particles of soil or with soil extracts. Active fermentation occurred with the formation of large numbers of bacteria, the aerobes formed a pellicle on the surface of the solution and the anaerobes gelatinous masses on the particles of calcium carbonate at the bottom of the solution. The aerobic organism had the characteristic form of *Azotobacter*, while the anaerobic genus was *Clostridium*; both appeared to be pure cultures. Both the organisms were active in repeated subcultures. While no nitrogen determinations were made nitrogen fixation was assumed following the identification of the organisms, and since the original media contained no nitrogen and there occurred abundant bacterial growth with active acid and gas fermentation. As a measure of bacterial activity aliquots of each medium were acidified with H_2SO_4, the volatile acids distilled and titrated against $N/100$ NaOH. The fermentation during May and June was greater than at any other time with both *Azotobacter* and *Clostridium*. Using the distillation technique the fermentation activities of both organisms in relation to the acidity of the medium were investigated. Both organisms showed reduced rates of fermentation at pH 4·5 as compared with those at 5·5, but while with *Clostridium* the reduction was 50% with *Azotobacter* the reduction was 90%. At pH 3·5 fermentation by *Clostridium* was reduced to 8% of that at 5·5, while *Azotobacter* was completely inactive.

Discussion

The values recorded in Table 1 for the percentage of water and organic matter in the samples emphasize the relationship between high humus content of soil and the amount of retained moisture.

The pH values bear no relationship to the total acidity of the soil samples, the total acidity decreasing rapidly with depth while the pH is lowest in the 10–17 cm. zone. The pH value is of course the resultant of the mixture of the strong and weak acids which are present as the result of the partial oxidation of the organic matter by the micro-organisms. Ecologically the maximum acidity of the soil is probably more important than the total amount of acid present, since, in general, nutritional studies show that it is the degree of acidity rather than the total acidity which is a controlling factor in plant growth. However, in examining the microbiological processes which occur in soil it is from values of the total acidity that most useful information can be derived. While the total acidity of the soil decreases with depth, the acidity/100 g. of organic matter increases rapidly, but the residual acidity (acidity/100 g. of organic matter after extraction of the soil successively with benzene, alcohol, water and 1% NaOH) decreases sharply. It may therefore be concluded that the microbe activity results in oxidations leading to the production of —COOH groups and to molecular degradations resulting in the formation of more soluble

substances. It is clear that not only are cellulose, hemicelluloses and pectins decomposed but also the lignin complex, and further investigations are being directed to the isolation of organisms which not only attack lignin but also open the benzene ring.

In the upper layer the acidity of the ligno-cellulose complex (residual acidity) is a considerable part of the total acidity, but in the middle and lower layers the acidity of this fraction is unimportant, and since the *p*H values vary little in these three layers it appears probable that the *p*H values of the samples are determined largely by the composition of the more soluble oxidation products. These soluble oxidation products are chemically ill-defined, but it is clear from the extended analysis of the upper layer that the ether-soluble organic acids are a relatively small fraction of the whole.

The E_5 value of 423 mV. places the soil in the lower range of the oxidizing group. Since it is not possible to analyse the redox systems in detail at present and to determine precisely the reaction or reactions to which the potential is related, its significance can only be considered in general terms. The oxidation of the organic matter in the soil by micro-organisms may be regarded as a series of linked redox systems catalysed by bacterial and fungal enzymes with molecular oxygen as the final hydrogen acceptor. The rate of oxidation will be determined by the rate at which oxidizable substrates are produced and the availability of oxygen, the latter being controlled in large measure by the diffusion resistances of the soil. At any one time, therefore, the rate of formation of oxidizable substrate and the rate at which this undergoes oxidation will determine the concentration of reduced and oxidized substances within the soil, and the ratio of the concentration of these two groups determines the soil potential. The relatively low value of E_5 suggests that, for this soil, oxygen availability is the factor limiting oxidation; nevertheless, the soil potential cannot be regarded as a direct measure of the rate of oxidation since it is certain that changes in the availability of oxygen affect the metabolic activity of the micro-organisms in a much more general manner than simply by increasing the oxygen available as the final hydrogen acceptor. In particular, the concentration of oxygen within the soil not only controls in some degree the constitution of the microbe flora but may also determine the nature of the enzyme system through which oxygen is utilized as the final hydrogen acceptor, quite apart from any stimulation of the growth and activity of those organisms which are more particularly concerned with the pre-oxidation stages of the organic breakdown. While in general, aeration of a soil (availability of oxygen), rate of oxidation and soil potential march together, these are only the outward manifestations of the complex metabolic processes of the soil micro-organisms.

While from the E_5 value it might be expected that the soil would contain nitrate this radical has never been detected. This places the soil in that group of oxidizing soils with a *p*H below 3·8, deficient in nitrates described by Pearsall (1938). Microbiological experiments reveal the reason for the absence of nitrate, since nitrite- and ammonia-oxidizing organisms are almost completely absent. This is probably the result of soil acidity, since earlier records state that the nitrifying bacteria are only present above *p*H 3·8–4·0. Further, since their activity does not confine them to a solid substrate as in the case of the cellulose-decomposing organisms, there is no reason to expect that they will occur in pockets isolated from the general acidity of the soil. The aeration of the soil is apparently not sufficient to promote the autoxidation of nitrite to nitrate which Corbet (1935) has mentioned as playing a more important part in the formation of nitrate in acid soils below *p*H 5 than the biological activity of *Nitrobacter*.

An interesting feature of this acid soil is the presence of micro-organisms which in pure culture do not multiply and are not metabolically active at *p*H values near to that of an aqueous suspension of the soil. The most important examples are a bacterium which decomposes cellulose and the nitrogen-fixing bacteria.

While the view that cellulose decomposition in acid soils is chiefly brought about by fungal attack is supported by observations made on this soil, it is of interest to isolate a bacterium capable of decomposing cellulose in aqueous media only at acidities much less than that of the whole soil. The degree of metabolic activity of the organism in the soil is as yet unknown, but it must be sufficient to maintain at least a small number of active colonies. Since chemical analysis has shown that oxidation, molecular degradation and increased acidity march together, it may well be that the *p*H at the surface of the cellulose fibre is higher than that in the general body of the soil. These organisms, therefore, whose substrate is a solid fibre may exist in isolated pockets and be little affected by the acidity of the whole soil. Such cellulose-decomposing micro-organisms may be widespread in acid soils, since a similar organism has been isolated from the *Eriophorum* peat located on the higher parts of the moor.

Nitrogen-fixing bacteria have been isolated from this soil, although the *p*H is much below that at which they can be grown in synthetic media lacking fixed nitrogen. There is, however, no evidence that they do fix nitrogen in the soil, and in view of the known *p*H limits of their capacity for nitrogen fixation in pure culture it would seem probable that they grow in acid soil by absorbing fixed nitrogen from the medium and by the fermentation of the carbohydrate present.

SUMMARY

1. A 'mor' bearing *Pinus sylvestris*, *Betula pubescens* and *Deschampsia flexuosa* was examined from the chemical and biological aspects.

2. Certain observations were made on the total acidity of the soil, the distribution of the acidity among the fractions of the organic matter in the humus layer, and of the acidity in relation to the depths of the samples from the surface.

3. A survey of microbiological activity revealed the presence of large numbers of bacteria and fungi. All the major groups of soil micro-organisms were well represented with the exception of the nitrifiers. These last were present in very small numbers, and this explained the failure to obtain positive reactions to tests for the nitrate ion.

4. In spite of the low *p*H a cellulose-decomposing bacterium and nitrogen-fixing bacteria were isolated.

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ON DIFFERENT TYPES OF UNGLACIATED AREAS DURING THE ICE AGES AND THEIR SIGNIFICANCE TO PHYTOGEOGRAPHY

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(With 7 figures in the text)

I. The theory of unglaciated areas during the last Ice Age in Scandinavia

Our knowledge of the existence of Ice Ages in the Northern Hemisphere is not very old. It dates from about the middle of the nineteenth century. Scientists in various parts of Europe found that the extensive masses of unsorted loose deposits, and the striated and polished rocks could not be explained in any other way than by assuming that a large ice sheet had existed which overrode the country, polishing the rocks and depositing moraine gravel.

The signs of glaciation are so abundantly present in almost all parts of Scandinavia that it very soon led to the supposition that the ice mass had covered the whole country and destroyed all plant and animal life. This was the 'tabula rasa' theory. As a consequence of the theory the present flora and fauna of Scandinavia were held to have immigrated after the Ice Age from the south and east. Further indication of this was found in 1870 by Nathorst who succeeded in discovering remnants of an arctic flora in southern Sweden in layers deposited just after the ice had retreated. Later many scientists found similar remnants in various places in southern Sweden, Denmark and southern and western Norway. It is remarkable that the frequency of these arctic floras in southern Scandinavia seems to decline towards the north. The remnants of arctic plants are much more scarce in middle Sweden and in the Oslo region in Norway than in southern Sweden and in Denmark.

One of the consequences of the 'tabula rasa' theory must be that since the Scandinavian flora is recruited from the south and east, all relationships of that flora must be to the south and east, and hence the Scandinavian flora must be a province of the middle or eastern European.

This, however, is not the fact, as far as the Scandinavian arctic and alpine flora is concerned. A strong relationship exists with areas west of the Atlantic, with Greenland and Labrador. Even Blytt, who otherwise accepted the 'tabula rasa' theory, felt uncomfortable about this fact; and after him Sernander (1896), Wille (see e.g. Wille, 1915) and Andreas M. Hansen, in the last decade of the nineteenth and the first of the twentieth centuries, advocated the view that the whole Scandinavian flora was not destroyed by the ice during the last Ice Age. Refuges must have existed along the Scandinavian coast where an arctic-alpine flora might have persisted during the Ice Age.

The existence of unglaciated areas during the last Ice Age was first confirmed geologically by Vogt (1913), who on geomorphological ground found that the outer part of the

Lofoten Islands had been ice-free and Ahlmann (1919) agrees with Vogt. Oxaal (1915) reached the same conclusions with regard to the island of Træna somewhat south of the Lofoten Islands, and Holtedahl (1929) suggested that the same view applied to some areas along the northern half of the Varanger peninsula in northern Norway.

In 1913 the eminent Swedish botanist Thore C. E. Fries introduced the concepts of unicentric and bicentric plant distribution areas in the flora of Scandinavia. As had been known for a long time, the areas of Troms and Torne Lappmark in northern Scandinavia on one hand, and the area of the Dovre and Jotunheimen mountains in southern Norway on the other, form centres of the arctic-alpine flora of Scandinavia. Unicentric plants are found in only one of these centres; bicentric plants are found in both but not in the area between. This peculiar distribution was explained by supposing that two unglaciated areas had existed during the last Ice Age, one in the outer part of Troms fylke in northern Norway, including the outer part of the Lofoten Islands, the other on the coast of Møre. The quaternary geologist Kaldhol (1932), and later also Undås (1939), assume the existence of ice-free refuges in the Møre area on geological evidence.

In later times Prof. Nordhagen, the Norwegian botanist, in a series of papers (see e.g. 1933 and 1935) has advocated the theory of the survival of plants in a number of places along the Scandinavian coast. He has been able to demonstrate this in a most convincing manner from examples, especially among species of the *Papaver radicatum* group (1931). He has also introduced geomorphological arguments unnoticed before and has raised lively discussion on these problems.

We are thus able to reconstruct in broad lines the history of the arctic and alpine flora of Scandinavia since the last interglacial period. During the last Ice Age the central part of Scandinavia was covered with ice, and only a few restricted areas along the coast were ice-free. In these areas a number of species survived the severe climate until the ice began to retreat. The survivors from the unglaciated areas followed the retreating ice up into the mountains. There they met another element which had followed the margin from the south and east. The present arctic-alpine element of Scandinavia is a mixture of these two elements.

This view is in all essentials correct, but calls for modification in some respects. We are able also to state more precisely the conditions under which the refugees had to live in the unglaciated refuges.

II. Unglaciated refuges during the last Ice Age outside Scandinavia

Let us first consider territories outside Scandinavia and what conditions were like there during the Ice Ages.

It is mainly the region around the North Atlantic which was most severely affected by the large quaternary Ice Ages. In the Behring Strait region no regional glaciation occurred, but only intense local glaciation in the mountains. Large parts of arctic Canada were also unglaciated (see e.g. Antevs, 1929). The major part of Canada and the northern parts of U.S.A. were, however, covered by ice. Yet, as was demonstrated by Fernald (1925), areas in Newfoundland and southernmost Labrador were ice-free.

As concerns northern Labrador, opinions differ. Odell (1938) opposed the view that ice-free nunataks in the region acted as refuges for any important flora, yet Abbé (1938) states that relic types among the vascular plants exist.

Turning over to Greenland, already in 1879 Kornerup had suggested the existence of unglaciated areas in western Greenland during the last Ice Age. This view was taken up by Warming (1888) and later by many others for almost all parts of Greenland (see e.g. Gelting, 1934). Of special interest is the statement of Koch (1928) that northernmost Peary Land (northernmost part of Greenland) was never glaciated.

In southern Greenland I have encountered facts which cannot be explained in any other way than by assuming that ice-free refuges existed there or in some area not far away. Of a flora of 160 species of macrolichens, one is endemic. Of the rest all except three are also found in Scandinavia. The macrolichen flora of southern Greenland has a relationship with the Scandinavian arctic-alpine macrolichen flora which approaches identity. As this identity can hardly be explained by migrations after the last Ice Age, the flora must be older than the last Ice Age, i.e. the flora must have survived the last Ice Age in southern Greenland or some area not too far from it.

Concerning Iceland, Thorarinsson (1937) shows us geomorphological reasons for supposing that large parts of north-western and northern Iceland must have been unglaciated during the last Ice Age.

Lynge (1938), by the study of lichens, has found that northernmost Spitsbergen was unglaciated; and in King Karl's Land (in eastern Svalbard) Nathorst (1901, 1910) found indications that the summits of the islands were never glaciated. These islands have a very interesting lichen flora.

Hadač (1941) shows us that parts of Bjørnøya were unglaciated during the last Ice Age, and that these parts contain a number of species of various plant groups which must have survived in place.

It appears that no one has assumed any part of Novaya Zemlya to have been unglaciated during the last Ice Age, but from what will follow it seems probable that parts of these islands were also ice-free.

In the British Isles unglaciated areas during the last Ice Age existed in southern England and western Ireland (see Discussion on British Flora, 1935). It seems probable that areas in western Scotland also were unglaciated.

In the Kola Peninsula, Ramsay (1898) finds evidence that parts of the northern coast, including Rybachin Peninsula, were unglaciated, but his view is strongly opposed by Tanner. There is botanical evidence in favour of Ramsay's conclusion.

In northern Siberia large areas were glaciated neither during the last Ice Age nor during the whole Pleistocene period (see e.g. Gerasimov & Markow, 1939; *Bolschoi Sovjetskii Atlas Mira*, 1937).

A general view on the last Ice Age may be expressed in the following way: the last Ice Age extended over vast areas in the Northern Hemisphere. Yet the ice was in most places unable to exterminate the whole flora. In most countries bordering the sea small refuges existed where plants were able to survive.

III. General remarks on the Quaternary Ice Ages

Traces of deterioration of the climate towards the Ice Ages may, according to Gerasimov & Markow (1939), be traced back in Russia as far as the latter half of the Oligocene. In this period the vegetation belts of central Russia began to migrate southwards. This process continued during the Miocene and Pliocene. Traces of local glaciations are found

in the mountains of the Caucasus and Pamir in Pliocene times, yet there are nowhere any signs of regional glaciation or development of ice shields. These are restricted to the Pleistocene or the Quaternary.

The Quaternary Ice Ages affected the whole world. Signs of large glaciations occur in all parts of Europe, in northern and central Asia including the Himalayas, and in northern America; in the Southern Hemisphere regional glaciations are found in Southern America, increased alpine glaciation occurred in the Andes, the southern part of New Zealand and parts of Australia were glaciated, and we have signs of a still more extensive glaciation in the Antarctic than we have to-day (see e.g. Antevs, 1928, 1929).

In most of the areas in the Northern Hemisphere where glaciations occurred, we have signs of separate Ice Ages interrupted by interglacial periods. In Europe and Northern America one Ice Age occurred in relatively recent times (20,000–30,000 years ago) which is called the Last Ice Age. The Last Ice Age was preceded by an interglacial, the Last Interglacial, which, according to Penck & Brückner (1909), is estimated to have lasted approximately 60,000 years. This figure they derive from estimations of the weathering of deposits from the Last Interglacial. The Last Ice Age was preceded by an Ice Age of greater extent than the last, the Great Ice Age. Before the Great Ice Age there was a long interglacial period, the Great Interglacial which, by the same methods by Penck & Brückner was estimated to have lasted 240,000 years. Before the Great Interglacial come one or more glacial periods, and the whole Quaternary period is estimated by Penck & Brückner at one million years. This has been confirmed by Kønigsberger (cited from Hulten, 1937), who, by measurements of helium in the mineral zircon, found the Quaternary period to have lasted between ½ and 1 million years.

IV. Some necessary concepts of glaciology. The retreat of the ice from Scandinavia

In recent times our information upon the life, development or requirements of glaciers has been much improved, chiefly through the work of Prof. Ahlmann and his pupils.

At first it is necessary to define the concept of the 'firn line' which is basic in glaciology and also has important bearings for our problems. The firn line is defined as the border between the accumulation area (the area where more snow is precipitated in winter than is melted away in summer) and the ablation area (the area where more snow is melted during the summer than is precipitated in winter). The firn line we can observe in the autumn just before the first snow falls. It is the border of the snow from last winter. The altitude of the firn line may vary from year to year, but is generally fairly constant.

It is necessary for the existence of a typical glacier that it has an accumulation area, i.e. that some area of the glacier is situated above the firn line. In regions where no summits reach above the firn line no possibilities of glaciation exist.

The morphology above and below the firn line of a glacier will be fairly different. Above the firn line more snow will fall than melts away in summer, and here the snow will ascend towards the sides (see Fig. 1), whilst the glacier will be concave. Accordingly the contours will be concave in relation to the direction of flow of the ice. The ice will flow from the sides towards the centre of the glacier, and no moraines will be deposited along the borders (i.e. there will be no marginal moraines).

Below the firn line the shape of a glacier will be convex and descend towards the sides.

Accordingly, the contours will be convex in relation to the direction of flow. The direction of flow will be from the centre of the glacier towards the sides. The ice will build up marginal moraines along its flanks and a terminal moraine in front.

The firn line is characterized by the contours of the glacier being straight. Great care and due appreciation of the morphology of the rock under the glacier are, however, necessary in judging the altitude of the firn line from maps of glaciers.

If for some reason the climate in an area improves so that a glacier loses its accumulation area, the glacier will be 'dead', i.e. it will be a relic from colder times, have no important movements and will gradually melt away. The last ice will be left generally in the place

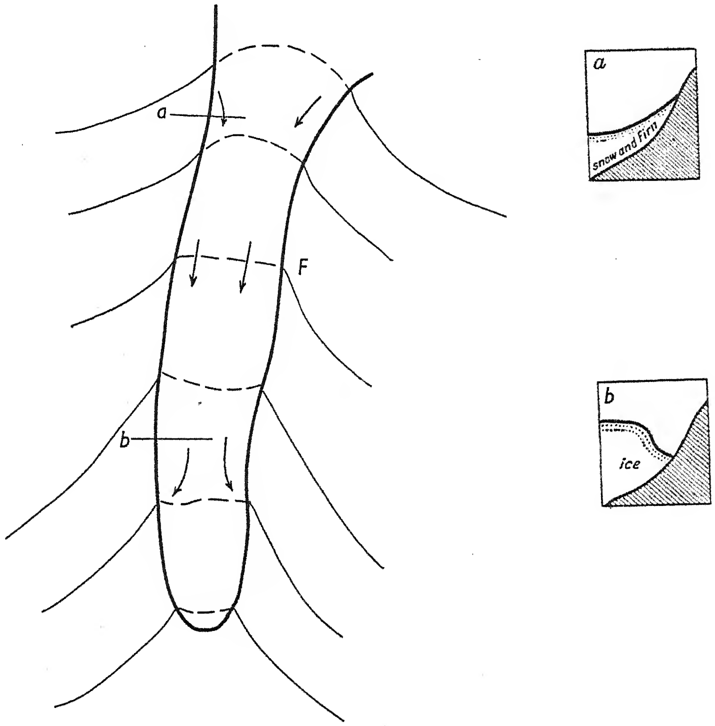

Fig. 1. Diagrammatic illustration of conditions on a glacier around the firn line. *a* and *b* sections of the border of the glacier above and below the firn line *F*. (*a* and *b* after Mannerfeldt, 1945.)

where the ice in the beginning was thickest. All the gravel contained in the moraine will either be brought to the sides of the glacier by melt-water and form marginal moraines, or be left on the surface or under the ice leaving a very irregular landscape after the ice has melted, a 'dead-ice landscape'.

In the area below the firn line a retreating glacier will deposit marginal moraines. These will be left as small ridged shapes distributed in fishbone patterns. The study of these and other late glacial deposits in Scandinavian mountains has been taken up and established by Ahlmann's pupil Mannerfeldt (Mannerfeldt, 1938, 1940, 1945).

Such marginal moraines are found in many parts of the Scandinavian mountains and often at high altitudes. What do these tell us about the conditions during the ice melting? First of all they indicate that during the period when the mountains thawed out of the ice,

the firn line was higher than the summits of the highest mountains, i.e. the ice-sheet was dead and accordingly had to behave like dead glaciers. The first thing which happened in Scandinavia was that the summits melted out of the ice; it is a wrong concept to believe that the ice retreated into the mountains. The last ice was left in Scandinavia where the large ice-sheet at the beginning was thickest.

The study of the marginal moraines yields information about the gradient of the surface of the ice when the moraines were deposited, and this informs us that in central and southern Scandinavia the last ice was left east of the high mountains. This has important bearings upon phytogeographical problems, especially that of the route taken by the flora following the margin of the ice from the south to reach those high mountains where they at present are found. When the ice retreated the arctic flora followed it, but could not persist at any great distance from the ice on account of the more boreal vegetation following behind. The arctic plants had thus a limited space along the ice margin in which to live. In the early stages of the retreat of the ice, the ice-sheet exercised great influence upon the climate and the region of arctic plants was wide. Such was the case in southern Sweden and Denmark, and accordingly it is not difficult to find remnants of an arctic flora in early deposits in these areas. As the ice withdrew the influence of the ice upon the climate diminished and the more southern flora could follow much more closely upon the ice, especially the pine and the vegetation accompanying it. The space of the arctic flora was thus restricted. All the while the arctic flora had to migrate after the ice. Accordingly, it is much more difficult to find remnants of the arctic flora in middle Sweden and southernmost Norway, and the representatives of the arctic flora which are found are generally species with light, windspread seeds. When the last ice which blocked the way to the mountains for the arctic flora melted away, the plants had still a long distance to migrate before they reached their goal. This must have increased tremendously the difficulties of this flora element in reaching the mountains. Yet undoubtedly a number of the arctic species managed to carry through the race, as we may conclude from their present-day distribution.

The flora from the western refuges had no such difficulties in reaching the high mountains.

V. The nature of the unglaciated areas in western and northern Scandinavia. Refuges of the coastal mountain type

In a previous section we have ascertained both on botanical and geological grounds that parts of the Troms and Møre areas were unglaciated during the last Ice Age. One may ask: 'Why only these regions?' 'Why not an area outside Bergen or Trondheim?'

This may be seen from a map of the relief, both the submarine and the mountain relief, of Norway. Scandinavia rests on a continental platform or shelf, submerged beyond the Norwegian coast. This shelf has a varying extension from 20 to 200 km. in width (see Fig. 2). The margin of the shelf is the borderline between the land mass and the deep ocean. The shelf is narrowest precisely in the Troms area (approx. 20 km.) and in the Møre area (approx. 40 km.). Just inland in each place rise high mountains with summits more than 1000 m. high. May this have something to do with our problem?

This issue has first been touched upon by Elfstrand (1927) who believed that the effect of the Gulf Stream, or the thermic effect of the deep waters during the Ice Age, must

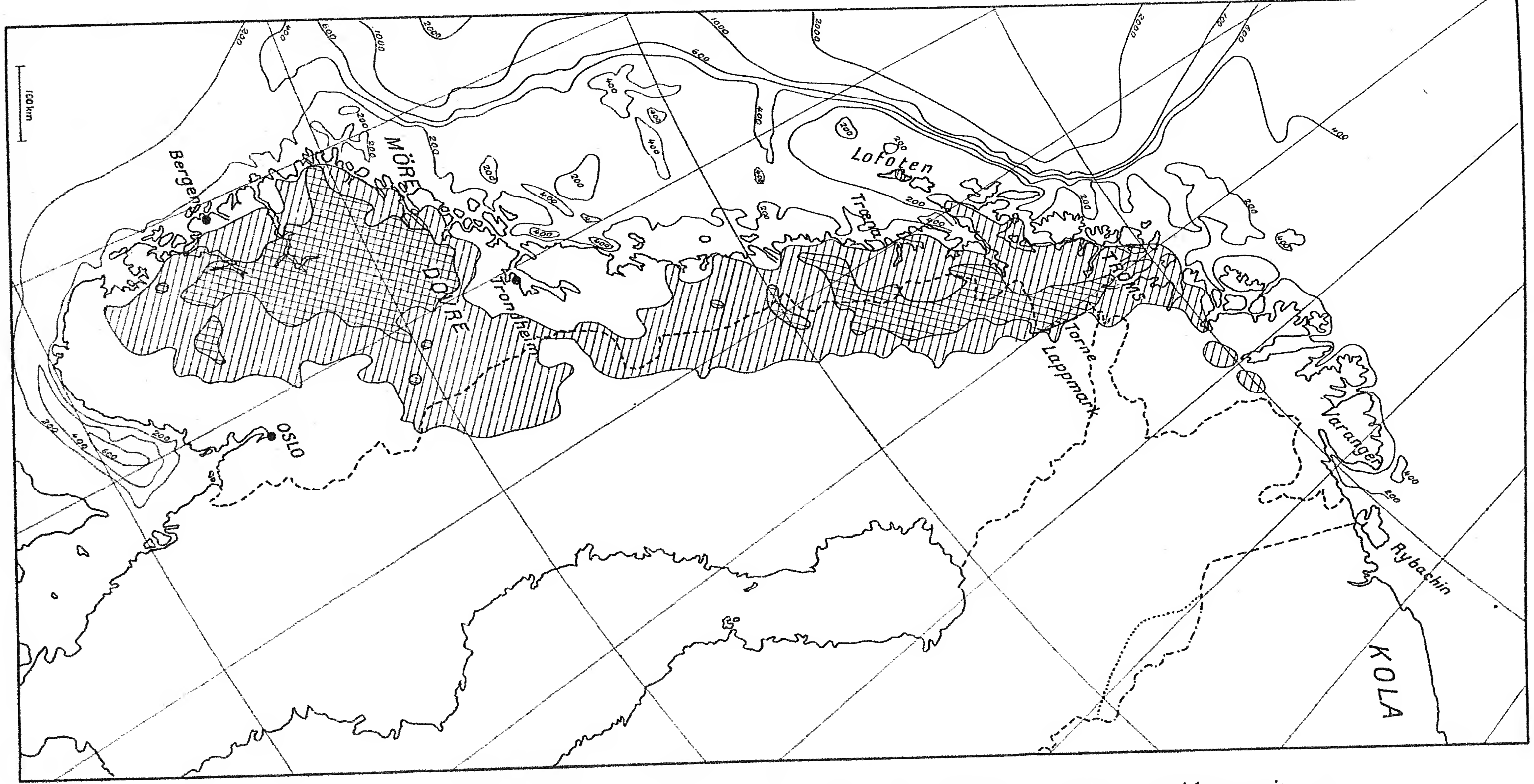

Fig. 2. Map of some features of the submarine and mountain relief of Scandinavia. Shaded: areas with summits more than 1000 m. high. Cross-hatched: areas with summits higher than 1500 m.

have been more important in these regions than elsewhere. I do not think this very important, and prefer to invoke other causes.

Thus it seems to me impossible to have a total glaciation under climatic conditions we know to occur on the earth, in a region where high mountains are situated near a deep ocean. The ice-shield cannot extend farther than to the border of the deep ocean. There the ice begins to float, breaks to pieces, and the icebergs are carried away by winds and currents. At the border of the ice under conditions where a large ice-shield is extending into the sea, the margin of the ice cannot have more than a limited height. From the border of the ice the thickness of the ice-shield increases towards the centre. The ice is plastic, and accordingly the gradient of the surface has a limit if the conditions are stable, and under such conditions to-day the gradient hardly ever exceeds 1 in 100 for any long distances, but is generally much less (1 in 200).

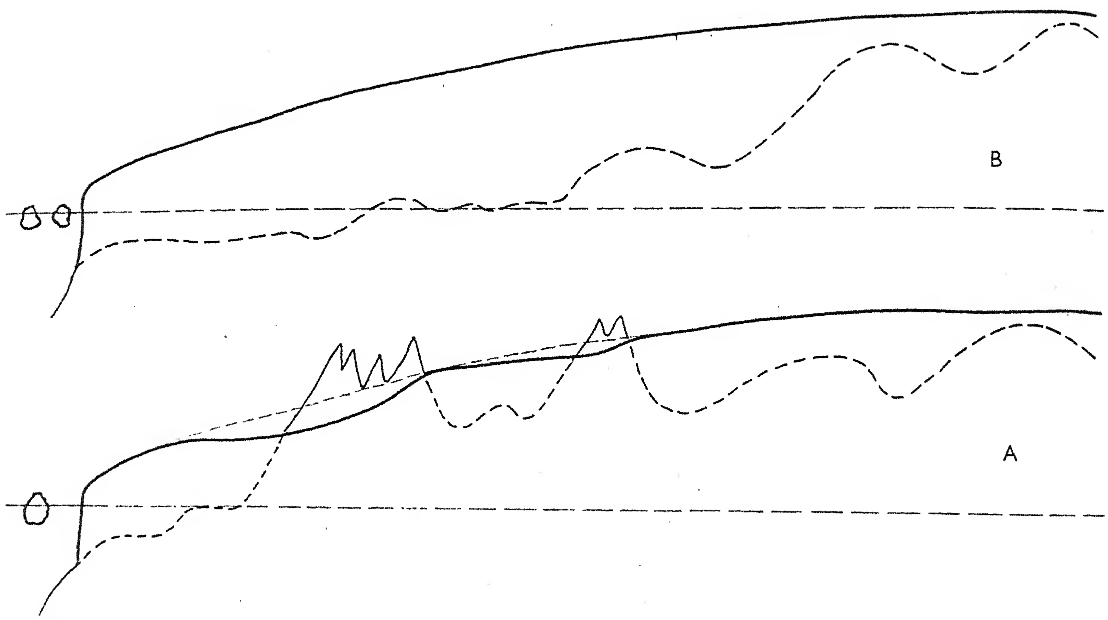

Fig. 3. Illustration of conditions during a glaciation of a land where: A, high mountains are situated near a deep ocean; B, high mountains are situated far behind the border of the ocean. (Diagrammatic in section.)

If we start from about zero m. or perhaps 100 m. at the border of the ice and go towards the centre of the ice-shield, ascending with a gradient of 1 in 100 we naturally find all summits more than 1000 m. projecting as nunataks (summits protruding over the ice-cover) until we come 100 km. from the border. That is to say that, if high mountains are situated near the border of deep oceans, the ice-shield will not have sufficient distance in which to grow thick enough to cover the high mountains (see Fig. 3A).

Where the high mountains are situated far from the border of the ocean (see Fig. 3B) the sheet will be able to grow thick enough to cover them.

This is no new knowledge. Holtedahl (1929, p. 28), dealing with conditions in the Antarctic wrote: 'The conditions now existing in the Palmer Archipelago and the adjacent districts of Graham Land show us for instance that we cannot in areas with similar topography (and with no broad upland) draw any simple boundary line for the greatest

extension of the ice, even assuming a most severe climate. We may judge that in such a coastal district with very dissected and rugged topography there will generally be no complete ice-cover.'

We know that in the Antarctic the ice has had greater extension than it has to-day, during an Ice Age which was probably synchronous with the last Ice Age in the Northern Hemisphere. Yet even during that period, the whole Antarctic can hardly have been totally glaciated. The Byrd Expedition collected on the nunataks a number of lichens which were examined by Dodge & Baker (1938). Their work proved that the Antarctic has a lichen flora of its own with a number of characteristic endemic macrolichens. As these endemics can hardly have been developed in the space of time since the last Ice Age, and as these species of lichens have never been found in adjacent countries, a lichen flora must have survived in the Antarctic during the last Ice Age. Consequently even during the last Ice Age, unglaciated areas must have existed in the Antarctic.

An unglaciated area caused by high mountains being situated near the border of a deep ocean we shall refer to as the *coastal mountain type*. As conditions in the Antarctic to-day teach us, in areas where a mountain complex or a mountain range is situated near a deep ocean, there will exist unglaciated areas almost down to the level of the sea on the side sheltered by the mountain complex from the ice flow.

VI. Unglaciated areas of the Scandinavian and the Antarctic types

We have found that in areas where high mountains are situated near the border of a deep ocean, unglaciated nunataks always exist. We may now ask: 'Which flora may be found in these nunataks?' 'Are they so completely barren to higher plants as the nunataks of the Antarctic?'

Opinions differ as to the possibility that a rich flora can exist upon nunataks. In the Antarctic only lichens and a few mosses are found. Lynge mentions a nunatak visited in Novaja Zemlya with a very poor flora of vascular plants. The Jensen nunataks in western Greenland at an altitude of 4000 ft. had a fairly rich flora (see Kornerup, 1879; Ostenfeld, 1926). The nunataks situated near the border of the large ice-sheet in southern Greenland have a rich flora. Especially the moraine on the sheltered side of the nunataks proves to be a good locality for vascular plants. We thus see that nunataks with a rich and with a poor vegetation both occur. Lichens are always present. We must therefore consider under what conditions a nunatak will contain a rich flora of higher plants.

An important factor must be the altitude of the firn line in relation to the foot of the nunatak. If the firn line is situated above the foot of the nunatak, the nunatak may contain a rich flora. The marginal moraine on the sheltered side of the nunatak, which is such a good locality for higher plants, occurs only under those conditions (see Fig. 4A). We shall refer to this category as nunataks of the Scandinavian type.

If the firn line is situated below the foot of the nunatak (see Fig. 4B) no marginal moraines will develop. Horizontal areas will be glaciated: elsewhere the wind blows the snow away. It must be very doubtful whether vascular plants can survive in places where the wind is strong enough to prevent the snow from accumulating. Only very few vascular plants can live under such conditions, but many lichens, especially microlichens survive. We shall call this type of nunatak the antarctic type, as all nunataks of the antarctic continent are of this kind.

Correspondingly we may refer to an unglaciated refuge during an Ice Age as a refuge of the Scandinavian type if the firn line is situated higher than the lowermost unglaciated area in the region during the severest period. A refuge of the antarctic type occurs where the firn line is situated below the lowermost unglaciated area, and this is commonly at sea level. In unglaciated refuges of the Scandinavian type, a number of higher plants can live, in an unglaciated area of the antarctic type generally very few higher plants will survive.

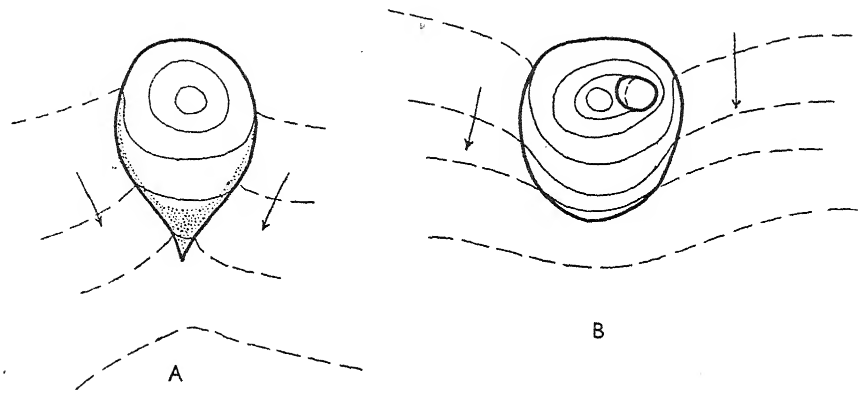

Fig. 4. Diagrammatic map of: A, nunatak of the Scandinavian type (firn line above the foot of the nunatak); B, nunatak of the antarctic type (firn line below the foot of the nunatak). The heavy continuous line marks the boundary of the nunatak, light continuous lines the contours of the nunatak surface, and broken lines the contours of the ice-sheet surface. The dotted area marks moraine.

VII. UNGLACIATED AREAS OF THE TUNDRA TYPE. THE FLORAS OF THE REFUGES OF THE COASTAL MOUNTAIN AND THE TUNDRA TYPES

We have found that the unglaciated refuges in the Troms and Møre areas were caused by the relief of the land mass; that they belong to the coastal mountain type. Are all unglaciated refuges from the last Ice Age of the same type?

That obviously cannot be true. On the north coast of Spitsbergen there is a broad shelf and no extraordinarily high mountains. The King Karl Islands reach approximately 300 m. altitude and rest on a shallow shelf. The unglaciated areas of northern Siberia, Canada and Greenland cannot be of the coastal mountain type.

These unglaciated areas are caused by other factors. During the last Ice Age most of the northern Atlantic was covered by sea ice. The ice acts meteorologically as a land mass. The areas situated far from the open sea will have a small precipitation, and very little snow will fall during the winter season. The refuges will be unglaciated because so little snow falls in winter that the insolation is sufficient to produce the energy necessary to melt it all away in the summer. This will be a type essentially different from the coastal mountain type. We shall call this type the tundra type.

Refuges of the coastal mountain type are found in western and north-western Scandinavia, probably in Scotland, Iceland, the southern half of Greenland (where the relief conditions to a high degree favour refuges of this type), and possibly in Labrador. Refuges of the tundra type are found in Siberia, possibly in the Kola Peninsula and Rybachin Peninsula, in northern Norway, Bjørnøya, Spitsbergen, in the northern half of Greenland

and in arctic Canada (see Fig. 5). I think it also safe to include Novaja Zemlya in this category.

In refuges of the tundra type the climate will be continental. In refuges of the coastal mountain type the climate may be atlantic or oceanic.

The two types of refuges will have different floras. If we want to know which plants probably were able to live in the tundra refuges we must go to the region where the climate to-day resembles the conditions which must have existed in the tundra refuges, i.e. northernmost Greenland and Canada. Typical of these regions are the lichens of the genera *Dactylina* and *Duforea* admirably mapped by Lynge (1933). If we take one of the species, *Dactylina ramulosa*, as an example (Fig. 6), we find that it has a distribution from the Behring Strait region to arctic Canada, the northern half of Greenland, Spitsbergen, Novaja Zemlya, Siberia and also central Europe. Also in the margin of the ice-shield in central Europe continental climatic conditions must have occurred.

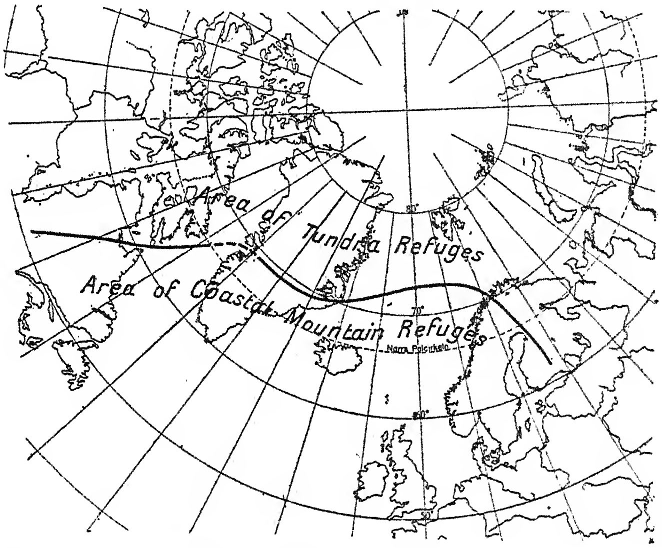

Fig. 5. Explanation in text.

There is a whole category of plants of the same or of approximately the same distribution. This distribution must have been caused by the fact that the tundra refugees could survive only in the tundra refuges but not in those offered by the coastal mountains. I regard the following as typical tundra refugees:

Tofieldia coccinea Richard
Arctagrostis latifolia (R.Br.) Griseb.
Dupontia Fisheri R.Br.
Pleuropogon Sabinei R.Br.
Deschampsia brevifolia R.Br.
Poa abbreviata R.Br.
Puccinellia angustata (R.Br.) Fr.
P. Vahliana (Leibm.) Th.Fr.
Braya purpurascens (R.Br.) Bunge
Carex ursina Dew.
Minuartia Rossii (R.Br.) Fenzl.
Arenaria ciliata subsp. *pseudofrigida* Ostf. & Dahl
Cerastium Regelii Ostf.
Melandryum affine J.Vahl coll.
Ranunculus sulphureus Soland.
Papaver Dahlianum Nordh.
Pedicularis lanata Willd. coll.

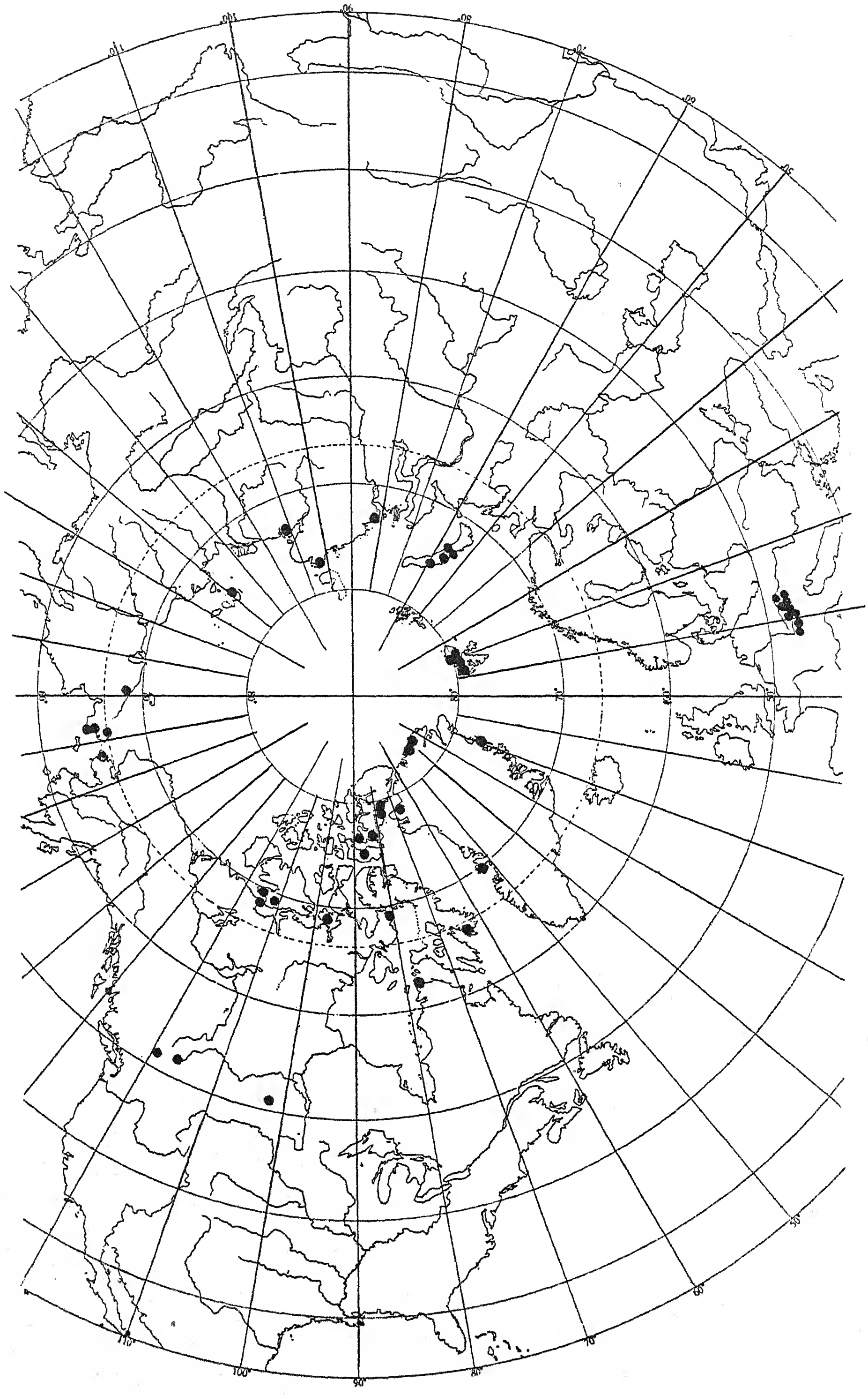

Fig. 6. Map of the distribution of *Dactylina ramulosa* (Lynge, 1933).

Eutrema Edwardsii R.Br.
Draba oblongata R.Br.
D. macrocarpa Adams coll.
D. subcapitata Simmons
Saxifraga setigera Pursh.
Potentilla hyparctica Malte.
P. pulchella R.Br.
Polemonium boreale Adams
Taraxacum arcticum Dahlst.
Dactylina arctica (Hook.) Nyl.
D. ramulosa (Hook.) Tuck.
D. madreporiformis (Hook.) Tuck.
Parmelia subobscura Vain.
Umbilicaria polaris (Schol.) Frey
Cetraria chrysantha Tuck.

Correspondingly there is an element or category of coastal mountain refugees.

As an example we may take *Alchemilla glomerulans* Bus. (Fig. 7). I regard the following species as typical coastal mountain refugees:

Botrychium lanceolatum (Gmel.) Ångst.
Allosurus crispus (L.) Bernh. coll.
Asplenium viride Huds.
Athyrium alpestre (Hoppe.) Ryl.
Polystichum lonchitis (L.) Roth.
Cystopteris montana (Lam.) Bernh.
Selaginella selaginoides (L.) Link.
Juncus arcticus Willd.
J. trifidus L.
Leucorchis albida (L.) E. Mey coll.
Phleum alpinum L. coll.
Deschampsia atropurpurea (Wg.) Scheele
Agropyron violaceum Lge.
Carex arctogena H.Smith.
C. Macloviana D'Urv.
C. brunnescens Poir.
C. rufina Drej.
C. atrata L.
C. bicolor All.
C. saxatilis L.
Sagina saginoides (L.) DT.
Stellaria calycantha (Led.) Bong.
S. crassifolia Ehrh.
Arenaria norvegica Gunn.
Viscaria alpina (L.) Don.
Thalictrum alpinum L.
Arabis petraea (L.) Lam.
Sedum villosum L.
Saxifraga Aizoon Jacq.
S. stellaris L.
Alchemilla alpina L.
A. glomerulans Bus.
Rubus arcticus L.
Epilobium lactiflorum Hausskn.
E. alsinefolium Vill.
E. Hornemanni Rchb.
E. anagallidifolium Lam.
Cornus suecica L.
Angelica Archangelica L.
Loiseleuria procumbens (L.) Desv.
Primula scotica complex
Gentiana detonsa Rottb.
G. aurea L.
G. nivalis L.
Veronica alpina L.
V. fruticans Jacq.
Thymus Serpyllum L. coll.
Rhinanthus groenlandicus (Chab.) Ostf.
Antennaria alpina (L.) Gaertn.
Gnaphalium norvegicum Gunn.
G. supinum L.
Erigeron boreale (Vierh.) Simm.
Thyrea radiata Smft.
Umbilicaria rigida (DR.) Frey
U. fuliginosa Hav.
Alectoria nitidula (Th.Fr.) Vain.

We know far too little of the ecology or requirements of arctic-alpine plants to be able to say which are the qualities that enable the tundra refugees to live in tundra refuges and not in the coastal mountain refuges and vice versa.

A characteristic feature of tundra vegetation is the lack of competition. The short summer, low summer temperature and the frequently extreme dryness which are consequences of the continental climate, allow no dense vegetation to develop. A species like

Saxifraga setigera with above-ground runners, living in the most favourable localities to be found in the Arctic, but nevertheless free from competition, would have little chance of survival in competition with a more southerly gramineous vegetation.

On the other hand, the coastal mountain refugees are often species with a high competitive power, occurring in dense meadows. In the coastal mountain refuges there was probably no lack of water in summer, and insolation was higher because the coastal mountain refuges are generally situated farther to the south. Among the coastal mountain refugees a number of snow-patch species occur (*Allosurus crispus*, *Athyrium alpestre*, *Cerastium cerastoides*, *Alchemilla* species, *Epilobium* species, *Veronica alpina*, *Gnaphalium*

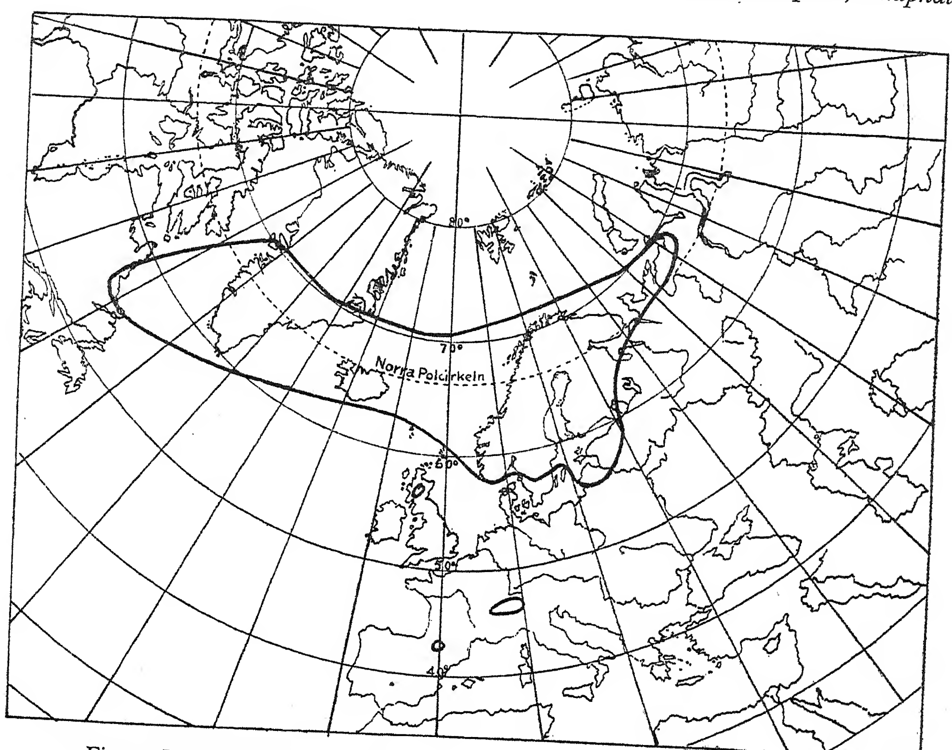

Fig. 7. Total distribution of *Alchemilla glomerulans* Bus. (After Samuelsson in *Acta Phytogeographica Suecica*, 1943.)

supinum and others). The necessary snow-cover could hardly be obtained in the tundra refuges with their small precipitation.

The following typology of the refuges is therefore proposed:

A. THE COASTAL MOUNTAIN TYPE caused by high mountains situated near the border of deep oceans.

I. *The Scandinavian type*. The firn line never descends to sea-level. Atlantic climate. Flora: Rich vegetation of vascular plants, mosses and lichens characterized by coastal mountain refugees.

II. *The antarctic type*. The firn line descends to the level of the sea in the severest period. Antarctic climate. Flora: Few or no vascular plants. Few mosses. Rich vegetation of lichens especially microlichens.

B. THE TUNDRA TYPE caused by small precipitation in winter. Firn line never descends to sea-level. Continental climate. Flora: Numerous species of vascular plants, mosses and lichens characterized by tundra refugees.

In this outline the use of the concepts of continental or atlantic (or oceanic) for conditions like those occurring in the Antarctic to-day has been replaced by the concept of the antarctic climate. The use of the concepts of continental and atlantic is based partly on the amount of precipitation, partly on the humidity of the air. These factors generally vary in a similar direction and are followed by characteristic features of vegetation and soil development. But under conditions of the most extreme cold the precipitation will always be low even if the relative humidity of the air is high and no development of soil and vegetation will be found. I will define an antarctic climate as one such that the firn line descends to the level of the sea in the region concerned. Only in areas with the firn line higher than the sea-level may one speak of atlantic or continental climate.

VIII. THE POSSIBILITY OF RICH FLORAS LIVING IN REGIONS WITH HEAVY GLACIATIONS

In the discussion about interglacial refugees in various regions one meets with the following problem: 'Is any really important flora able to persist in regions of heavy glaciation in the limited refuges generally available? Would not the mere proximity of the vast icesheets affect the climate so severely as to destroy vegetation composed of any but the hardiest plants?'

Attempts have been made to compare conditions in Scandinavia during the last Ice Age with conditions to-day in Alaska, where even forests can live close to the great glaciers (Stejneger, 1908), or with southern Greenland where small birch forests live close to the ice, or with western Scandinavia where apple trees are blooming against a background of permanent ice. These examples are pointed out by those who believe in the persistence of large floras in the refuges. Others, less extreme, choose their comparisons from Spitsbergen, northern Greenland or the Antarctic.

The question must be put in the following form: 'Under what conditions can a southern flora persist in regions of heavy glaciation?'

The most important factor for plant growth is the summer temperature. The plants are not appreciably affected by the winter temperature provided that they can stand the winter minimum. What is important is the length of the summer and a relatively high temperature in the vegetative period.

Let us choose as an example a region with a firn line at 500 m. Let us increase the summer temperature and see what changes of other climatic factors are necessary to keep the firn line constant.

The altitude of the firn line is mainly dependent on the melting of snow in the summer on the one hand, and the amount of precipitation in winter on the other. The melting of snow in summer is largely dependent upon the summer temperature and the length of the summer. If the summer temperature increases it is necessary that the precipitation in winter also increases to keep the altitude of the firn line constant.

If, alternatively, the precipitation in an area increases it is necessary to increase the summer temperature to keep the altitude of the firn line constant.

We must conclude from this that in refuges with a firn line above sea-level, a high summer temperature is necessarily combined with a high precipitation, i.e. atlantic climate.

If, on the other hand, we have refuges in areas of atlantic climate and reasons to believe that these refuges were not of the antarctic type we must expect that more southern types had the possibility of existing in these areas, and the more so the more atlantic the climate was. Accordingly, one may expect that relatively southern types were able to exist even in limited refuges on the western coast of Scandinavia and especially in the British Isles during the last Ice Age.

IX. Concluding remarks

The thesis we have developed affords part of the solution of the problem of the southern Greenland macrolichen flora. As mentioned earlier the southern Greenland macrolichen flora is almost identical with the Scandinavian. This can be explained by the following factors:

(1) The macrolichen floras of Scandinavia and Greenland date from a period when a closer connexion than that of to-day existed between the European and the American floras.

(2) The factors of selection operating in both regions during the last Ice Age were almost the same and different from those, for instance, in Novaja Zemlya and the Alps.

As to point (1) we have reasons to believe that this is the fact. In interglacial layers in Europe fossils of species of vascular plants extinct in Europe but occurring in America are found. And if the western arctic elements in the Scandinavian alpine flora are to be regarded as survivors from the last interglacial it must be part of the wider supposition that the flora of Europe during the last interglacial had a more American character than it has to-day. The cause of this is a problem of its own. I cannot venture to say whether the Wegener hypothesis, the hypothesis of a land bridge over the Faeroes to Iceland, or any other hypothesis can solve this problem.

As to point (2), the refuges both in southern Greenland and in Scandinavia during the last Ice Age were of the coastal mountain type and the Scandinavian subtype.

We have all the time spoken about the Last Ice Age. We know that before the Last Ice Age there was a still more severe glaciation, the Great Ice Age. Whether the plants were able to survive the Great Ice Age in Scandinavia, Scotland or in other areas of the coastal mountain type is a more difficult problem. If we postulate that the relief 100,000 years ago was approximately the same as to-day, we may conclude that in some areas total glaciation did not occur. At least some few nunataks existed. The areas which we are able to prove were unglaciated at the outer coast of Møre, at Træna and in Finmark were doubtless glaciated during a previous glaciation, for large submarine ice-formed valleys occur outside these areas, and these could hardly have been formed without the existence of a large ice-sheet overriding those areas. This is not the case with the Lofoten Islands. There are, as far as I know, no signs to be found on the shelf outside these islands of any regional glaciation which would make it necessary to conclude that these areas had been totally glaciated at any time.

One problem must be pointed out. We have found that the existence of a dominating western arctic element of the alpine flora of Scandinavia can be explained by the theory of the survival of plants during the Last Ice Age. But if the whole flora was exterminated during the Great Ice Age in north-western Europe and no closer connexion between America and Europe existed after that time, the Scandinavian alpine-arctic flora still would be a province of the middle European. From a phytogeographical point of view we must consequently either postulate that a closer connexion between north-western

Europe and north-eastern America existed during the last interglacial, or we must believe that an arctic-alpine flora could survive during the great Ice Age in some refuges in north-western Europe.

To solve these and other problems a new line has been taken up during the last few years by Americans and Swedes. New methods of deep-sea borings have been evolved. If they are successful they may disclose the age of the Atlantic Ocean and whether any part of it was emerged during the Pleistocene period. Enumeration of moraine horizons can provide better information of the number and extent of the Ice Ages, and studies of fossils from interglacial and glacial deposits may yield information of the climate throughout the whole period.

During the great Ice Age many of the refuges of the Northern Hemisphere were doubtless of the antarctic type, where only numbers of microlichens could live. A closer study of the arctic and subarctic microlichen flora, already started by Prof. Lynge, will probably give us information of older phytogeographical relationships of the North Atlantic area than will be provided by studies of other groups of plants.

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MECHANICAL STIMULATION AND RESPIRATION IN THE GREEN LEAF

VI. THE RELATIONSHIP BETWEEN STIMULATION EFFECT AND TEMPERATURE

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(With 6 figures in the text)

Introduction

In previous papers (Audus, 1935, 1939, 1940 and 1941) it has been demonstrated that the respiratory system of green foliage leaves is very sensitive to slight mechanical deformation of the cells, such as may be brought about by bending or gently rubbing the leaf. The main result of such treatment is a considerable stimulation of the rate of respiration (CO_2 evolution), and a slow recovery over a period of days. The relationships of these effects to oxygen concentration (Audus, 1940) suggested that the action was centred on the oxidative processes of the total respiration sequence, which starts with reserve mobilization and ends with CO_2 evolution.

The work to be described was carried out to elucidate the temperature relationships of this traumatic sensitivity of respiration in the hope that this might throw still further light on the mechanism of the stimulation.

Materials and methods

The material used was cherry laurel (*Prunus lauro-cerasus*), as in earlier work. Uniform samples of leaves of the current year's growth were obtained from the same bushes, and then respiration followed in the dark by means of the Pettenkofer technique with a Blackman air commutator (see previous papers). Continuous 3-hourly readings of CO_2 evolution were obtained for periods of weeks. The respiration chambers were the simple metal ones used in the original experiments. For observations at temperatures of 32·5 and 22·5° C. the chambers were immersed in a well-stirred water-bath, heated electrically, and controlled for temperature by a mercury-toluol thermostat. For 12·5° C. a similar thermostatically controlled bath was used, but it was found necessary to arrange for an additional slow stream of tap water (temperature 10–11° C.) to run through the bath. By careful adjustment of the rate of water flow temperatures could be maintained to within 0·2° of 12·5° C. for indefinite periods. Observations at 2·5° C. were carried out in a large refrigerator (150 cu.ft. capacity). Lack of space precluded the use of the air commutator, and Pettenkofer tubes were changed by hand during the day, 12 hr. readings being taken over the night periods. In all experiments the air used for passing over the leaves was led in from outside the laboratory to avoid gas contaminants.

Stimulation of the leaves was carried out by hand as previously described (1935). Thus temperature conditions during stimulation varied somewhat, the leaf samples stimulated

at the higher temperatures being exposed for a short time ($\frac{1}{2}$–1 min.) to room temperatures during stimulation. That this momentary exposure to a lower temperature did not alter the development and subsequent intensity of the respiratory effect has been shown by experiments on stimulation *in situ*, using the special chamber described for work in various gas mixtures (1940). For stimulations at 12·5° C. (approximately room temperatures) and 2·5° C., these momentary drops in temperature did not occur.

Experimental procedure consisted essentially in following, from the time of plucking onwards, the starvation respiration of a leaf sample (30–40 leaves) at one temperature and stimulating after a steady state had been reached on the protoplasmic phase. This protoplasmic phase of the starvation respiration drift is the steady, slowly falling phase following the phase of initial adjustment (floating phase) (for details see Blackman, 1908 and Godwin, 1926). This second phase corresponds with the slow steady exhaustion of reserves (mainly starch) before the final accelerated general breakdown of the senescent phase. As far as possible all experiments were carried out under the relatively constant conditions of this protoplasmic phase. After recovery from the stimulation the temperature conditions were changed abruptly by rapid transfer of the chamber to the new conditions. As will be seen later, temperature transition effects on the respiration were always obtained, and stimulation at the new temperature was therefore generally postponed until a steady equilibrium rate of respiration was attained. One experiment only was carried out entirely at 32·5° C.

The effects of temperature on the normal respiration

It is an old established fact of physiology that, broadly speaking, biochemical processes follow the van't Hoff law, and this has been demonstrated many times for plant respiration. It would be surprising, however, if, in a process involving such a relatively complicated sequence of distinct chemical reactions, steady and unvarying values of Q_{10} should be obtained. Any small differences of Q_{10} between individual components of the reaction chain will cause variations in the gross Q_{10} with changing conditions of temperature. In addition, any changes induced in the effective concentrations of reactants (initial or intermediate substrates) will greatly modify the temperature effects. This has been conclusively demonstrated by Hopkins (1924) and Barker (1933), who showed that an accumulation of sugar in the potato tuber at temperatures of $-1°$ C. offset the normal effect of temperature and even gave rise to a negative Q_{10} in the temperature range 0–2° C. (Hopkins). Barker also demonstrated the accumulation of a respiratory depressant at low temperatures which reduced still further the apparent gross Q_{10}.

That the same broad principles hold in the cherry laurel was shown by Roux (1929). In these leaves complex temperature transition phenomena were observed, the nature of which varied with the degree of maturity of the leaves concerned. Analytical evidence was obtained of both hexose and sucrose accumulation at low temperatures. In order to explain his transition effects, however, Roux postulated the need for two respiratory substrates, starch and sucrose, the hydrolysis of the latter having a much higher Q_{10} than that of the former. This somewhat complicated theory, however, is far from convincing. In the following discussion of results attempts will be made to demonstrate that the facts are capable of a much simpler explanation.

All experimental results are brought together in Fig. 1. Here graphs of respiration rates are plotted against time of starvation as double lines. These two lines represent the

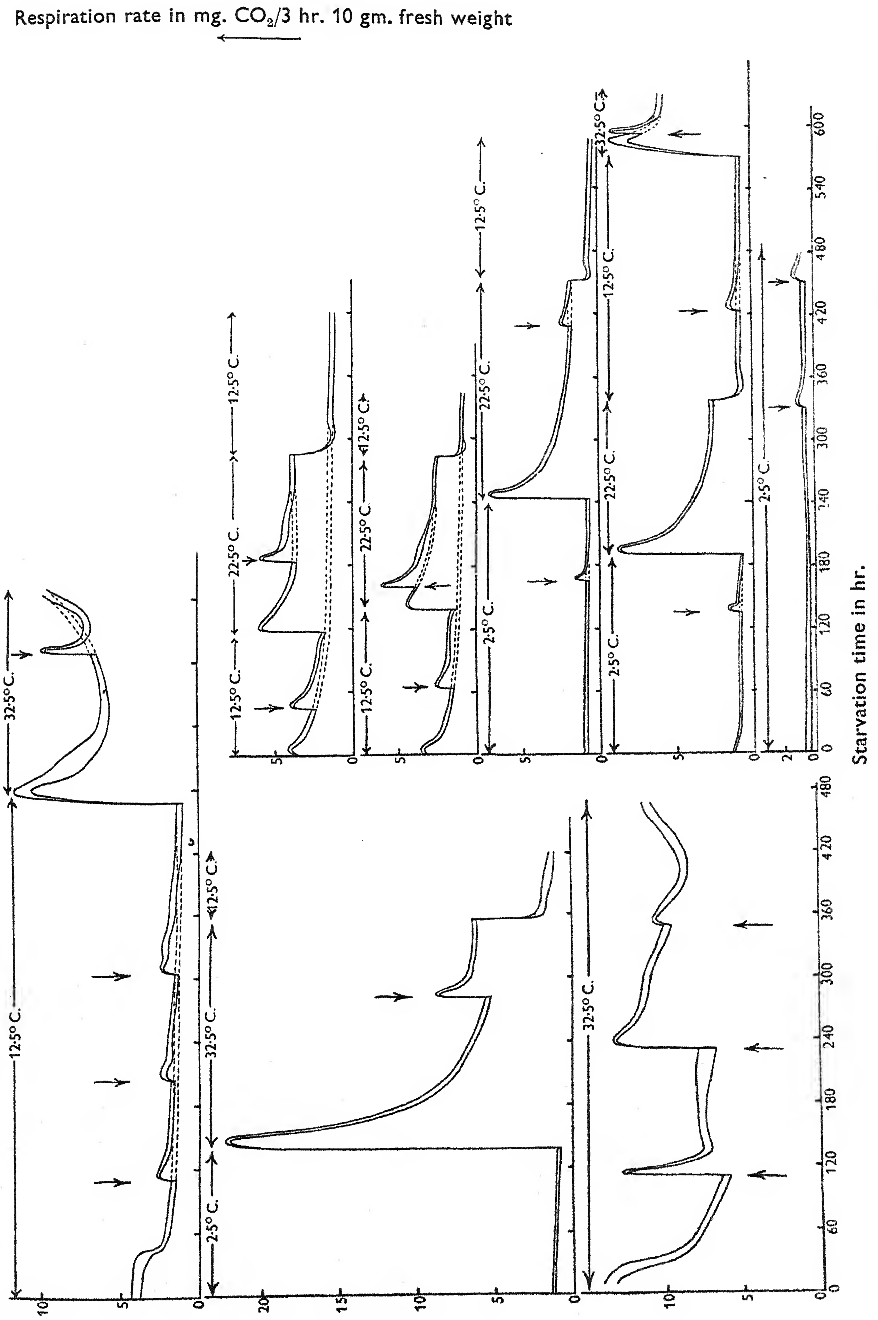

Fig. 1. Smoothed respiration curves for cherry laurel showing temperature-transition effects and the effects of mechanical stimulation. The parallel lines represent the limits of scatter of individual 3 hr. respiration readings.

limits of scatter of the individual 3-hourly respiration readings, which have been omitted for the sake of simplicity. Temperature treatments are marked, and the times at which stimulation occurred are also shown by the small vertical arrows. In the first place, change from one temperature to a higher one gives rise to characteristic transition curves, which are similar to those obtained by Roux. There is an immediate and considerable rise in the rate of CO_2 output, followed by a smooth fall, over a period of days, to a new

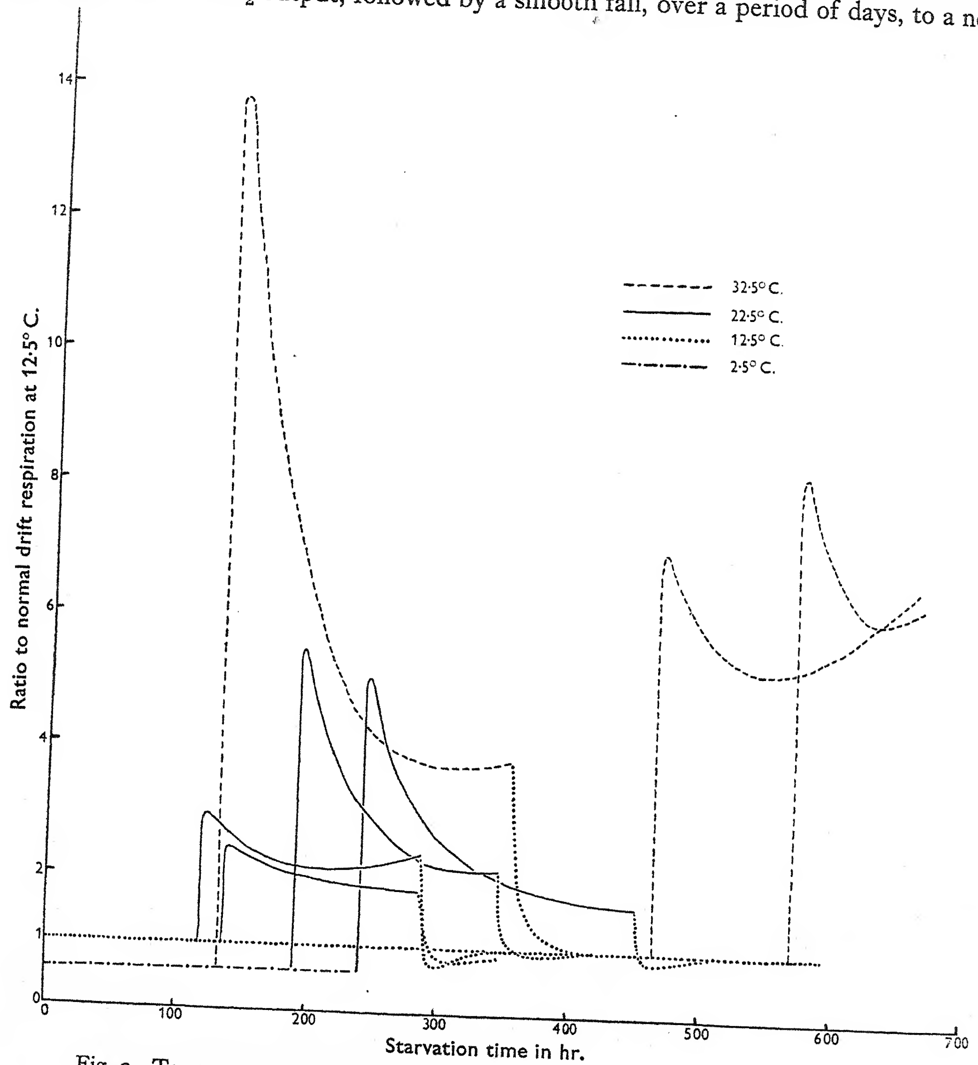

Fig. 2. Temperature transition effects on the respiration drawn as ratios to normal drift rates at 12·5° C.

level value. The magnitude of this new value is closely related to the actual temperature, whereas that of the initial peak of the transition curves depends also on the nature of the transition. These two facts are clearly brought out in Fig. 2, where the smoothed average respiration rates have been plotted as ratios to the normal starvation respiration drift at 12·5° C. Here it will be seen that the final 'equilibrium' values, after the transition effects, are all similar for the same temperature, and are independent of the nature of the

transition.* The heights of the initial peaks, however, vary with the nature of the transition, being directly correlated with the rise in temperature at that transition. These graphs also bring out the nature of the reverse transition effects, i.e. from high to lower temperatures. Here the final drift value at the new temperature is reached only after a reversed type of effect in which the respiration falls rapidly to a minimum and then rises

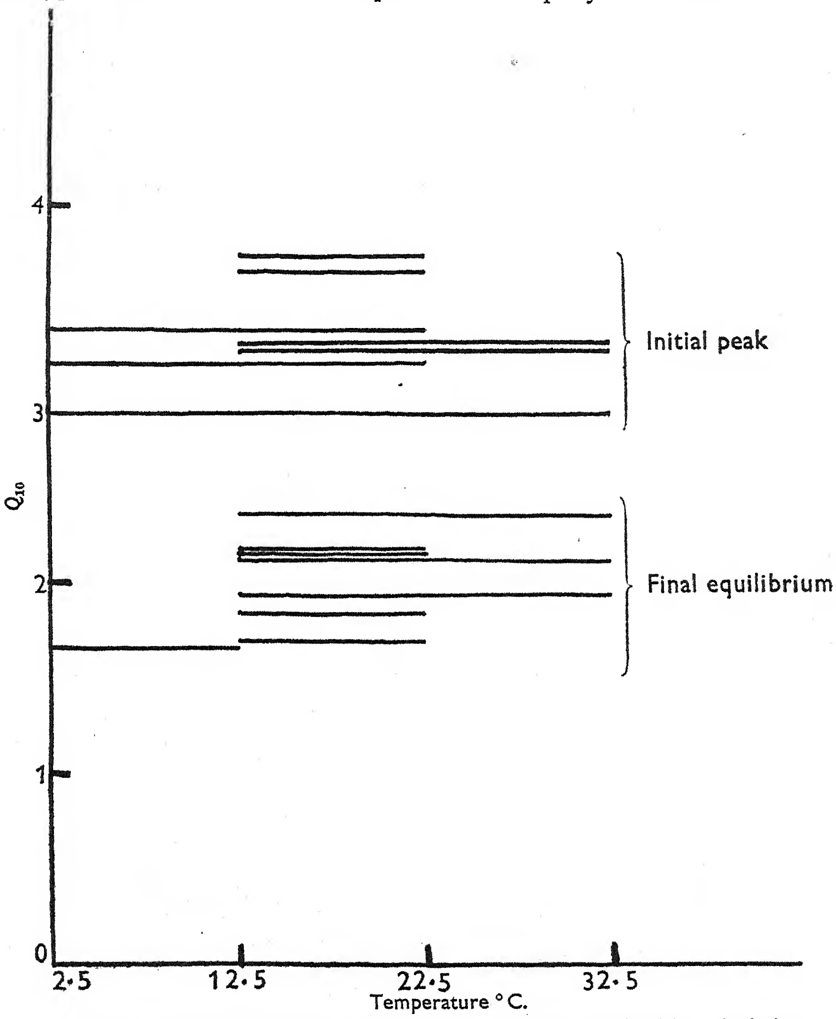

Fig. 3. Figure showing the two sets of values of Q_{10} obtained by calculation from temperature transition curves.

slowly up to the final equilibrium value. These latter transition effects, though small, are quite significant.

From the first type of transition, i.e. from low to higher temperatures, two values of Q_{10} can be obtained, namely, that from the initial peak intensity and also that from the final level drift after the transition effect. These two values have been calculated in all cases where applicable and are plotted graphically in Fig. 3. These figures show that the values fall about averages of 3·25 (initial peak) and 2·15 (final equilibrium) respectively.

* The final rise in 'equilibrium' drift value for the two transitions from 12·5 to 32·5° C. at the extreme right of the graph is due to the onset of the senescent phase and leaf yellowing.

These results can be explained completely on the assumption that here we are dealing with a chain of chemical reactions and that the actual Q_{10} differs from component to component in the chain. Thus we may express the respiratory chain of reactions in its simplest form as

$$\text{Reserve (starch)} \rightleftharpoons S \rightarrow CO_2 + H_2O.$$

Starch, which is the ultimate substrate in the above equation, is probably the chief respiratory reserve used during the protoplasmic phase of the starvation respiration of leaves, on which the above experiments were performed. This starch is hydrolysed to a simpler substrate S, which may be a hexose sugar. That this reaction is reversible seems most probable from the work of Hanes (1940*a*, *b*) with phosphorylases isolated from the pea and the potato. This substrate S, which may be the glucose-1-phosphate of Hanes, then breaks down by a second series of reactions, ultimately involving oxidation and the final evolution of respiratory CO_2. The gross rate of this final reaction may be determined by the concentration of S. Barker (1933), for example, has shown that a typical enzymatic rectangular hyperbola related the rate of respiration to sugar concentration in the potato tuber. If these two suppositions are correct, then it can be shown that the concentration of S will reach an equilibrium value at each temperature when the net rate of hydrolysis equals the net rate of oxidation of S. Thus, following Haldane (1930), it can be shown that for the reversible $St \rightleftharpoons S$ reaction, when not at equilibrium, the rate of change (here starch hydrolysis) is equal to the following expression:

$$\frac{K_1 V St - K V_1 S}{K K_1 + K_1 St + KS},$$

where V and V_1 are the maximal rates of starch hydrolysis and S condensation respectively in the absence of the other reactant, K and K_1 are the Michaelis constants for these two reactions and St and S are the momentary concentrations of starch and intermediate substrate (sugar).

It seems likely from a consideration of the level respiration drift curves that the effective value of St is maintained constant, irrespective of the total amounts of starch grain in the organ. This suggestion is supported by the results of Hanes (1940*a*, *b*). If, in addition, and for the sake of simplicity in drawing the curves, we assume that KS is small compared with $KK_1 + K_1 St$, we can neglect it in the expression, which then simplifies to

$$X - YS,$$

where X and Y are constants and equal to

$$\frac{K_1 V St}{K_1 K + K_1 St} = \frac{V St}{K + St} \quad \text{and} \quad \frac{K V_1}{K K_1 + K_1 St}$$

respectively.* We can now represent graphically the relationship of starch hydrolysis and respiration (sugar oxidation) to sugar concentration. This is shown in Fig. 4, where sugar production from starch at various temperatures is drawn, according to the above expression, as straight lines cutting the sugar axis at the equilibrium concentration P. This, of course, is the equilibrium concentration in the absence of any respiratory process acting on the sugar. The sugar breakdown in respiration is shown as following a typical enzymatic rectangular hyperbola with sugar concentration. Where these two rates are equal,

* The neglect of KS in relation to $KK_1 + K_1 St$ in this expression produces a straight line instead of a shallow S-shaped curve, and makes no difference to the general truth of the conclusions drawn.

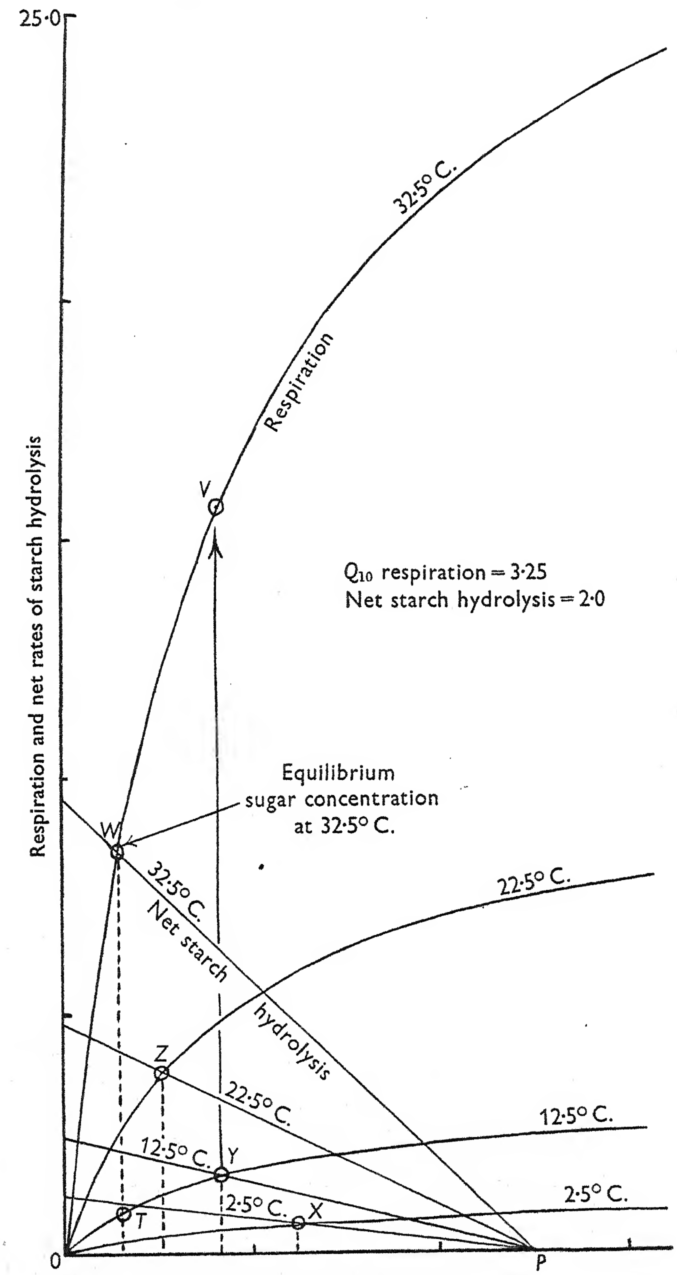

Fig. 4. Theoretical curves showing the interrelationship of respiration, reserve hydrolysis, sugar concentration and temperature (for explanation see text).

i.e. the point at which these two graphs cut, will represent the equilibrium concentration of sugar in the leaf on the protoplasmic phase.

Increase of temperature will increase both these rates. If the Q_{10} of both reactions is the same, then the curves will continue to cut at the same value of S. If, however, the

Q_{10}'s differ, then the equilibrium value of S will vary with temperature, as shown by the four sets of curves, which have been drawn on the assumption that the Q_{10} for the starch$\rightleftharpoons$sugar reaction is 2 and that for respiration is 3·25. In this case the equilibrium value of S decreases with rise in temperature, as is shown by the curves for increasing temperatures cutting at points of decreasing sugar concentrations X, Y, Z and W.

We can now deduce what will happen at a transition from the low-temperature conditions, e.g. 12·5° C. represented by curves cutting at Y, to the conditions at a higher temperature, e.g. 32·5° C. The rate of respiration will rise immediately on transition from point Y to point V, since the sugar concentration remains unchanged during the short time of the transition. The Q_{10} obtained from these peak values will therefore represent the effect of temperature on the respiration process itself. The respiration rate is now well in excess of the hydrolysis rate. Sugar concentrations will therefore decrease, the respiration falling correspondingly along curve VW until the new equilibrium value of S is reached at point W. Measurements of Q_{10} from these values will fall between the true Q_{10} for respiration and that for reserve hydrolysis.

If the foregoing represents the true conditions existing in the leaf, then the total CO_2 evolved in excess of the level of the final equilibrium values in the transition effect should be accounted for entirely by the extra sugar respired in bringing down the sugar concentration to this new equilibrium value. In other words, this change in concentration should be calculable from the transition curves. The results of such calculations appear in Table 1.

Table 1

Exp.	Transition data °C.	Area of transition curve above final equilibrium value mg. CO_2 per 10 gm. fresh weight	Area in terms of mg. hexose respired per 10 gm. fresh weight	Temp. change °C.	Diff. in sugar conc. (hexose) %
I	12·5–22·5	19·43	13·24	10	0·132
II	12·5–22·5	19·44	13·24	10	0·132
III	2·5–22·5	42·7	29·2	20	0·292
IV	2·5–22·5	61·05	41·7	20	0·417
V	2·5–32·5	196·0	133·8	30	1·338
VI	12·5–32·5	62·1	42·5	20	0·425

It will be seen that the changes in concentration of sugar (calculated as hexose) necessary to account for these large transition effects are relatively small and are directly correlated with the magnitude of the temperature change at transition. They are of the same order as those observed in the sweetening and de-sweetening of potato over the same temperature range noted by Hopkins and Barker. Roux also obtained biochemical evidence that such a sweetening takes place, although the sugar increase was attributed mainly to sucrose.

Similarly, on transition from a high to a lower temperature the respiration will fall rapidly from point W to point T and then rise slowly along curve TY until it again reaches equilibrium at the final sugar concentration (point Y).

STIMULATION EFFECTS

A cursory glance at the graphs of Fig. 1 shows that stimulation gives the characteristic effects on the respiration at all temperatures, and that the magnitude of the effect bears a direct relationship to the intensity of the respiration. Analyses of these effects are seen

in Fig. 5, where the percentage rise is plotted against the starvation time and the temperature respectively. The percentage rise is the percentage increase in the respiration on stimulation measured at the initial peak value. From a consideration of these two graphs two points are apparent:

(1) There is no significant change in the value of the percentage rise over the range of temperatures studied, i.e. stimulation causes the same relative increase in the respiration at all temperatures.

(2) The large scatter of values at any one temperature in the temperature curves is partly due to starvation-drift phenomena (Audus, 1935) in which the sensitivity of the leaf to stimulation falls away with starvation. One effect of temperature is, however, apparent from these curves, i.e. that high temperatures apparently greatly accelerate this rate of loss of sensitivity. Thus at low temperatures (2·5 and 12·6° C.) there is very little downward drift, whereas at the higher temperatures the percentage rise falls away very rapidly with starvation.

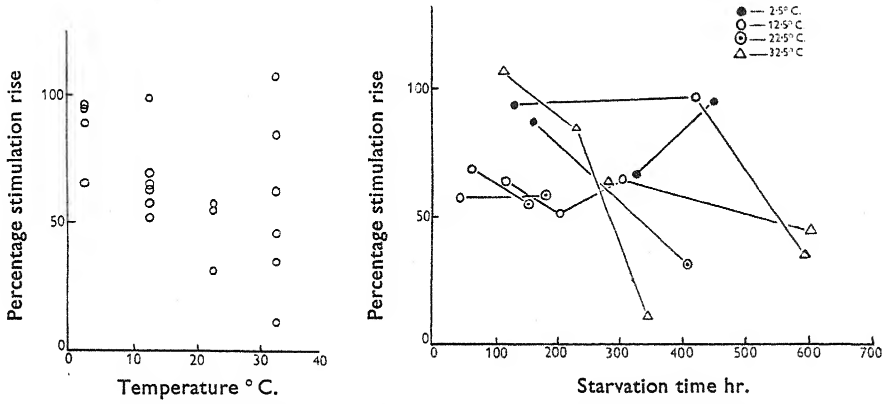

Fig. 5. Curves showing relationship of percentage rise of respiration on stimulation to temperature and starvation time.

What is the significance of these results when regarded in the light of conclusions drawn from the temperature-transition effects? It would seem that stimulation could act in two ways on the respiratory system as expressed in its simplest form on p. 248. First, it could accelerate the net rate of hydrolysis of reserves thereby pushing up the equilibrium sugar concentration and thus increasing the respiration rate. Secondly, it could stimulate the rate of oxidation of sugar by acting on a component or components of the respiratory system subsequent to S. Let us take up these two alternatives in order and see how they fit in with observations.

Fig. 6 has been drawn to show the possibilities outlined above. SP and OR are the net hydrolysis and respiration curves for a temperature of T° C., and $S'P$ and OR' are similar curves for a temperature of $T+10$° C., assuming, as in the previous section, a Q_{10} of 2 and 3·25 for these two processes respectively. A and E represent the equilibrium concentrations of sugar at these two temperatures. Taking the first of the above two possibilities, curve SsP shows the new stimulated hydrolysis curve (100% increase) at T° C. Assuming that this increase in the hydrolysis rate takes place immediately after stimulation, then hydrolysis becomes suddenly in excess of respiration, and the sugar

concentration will rise until a new equilibrium value is reached in the leaf at point B at temperature $T°$ C. This will not happen immediately since the leaves will take an appreciable time to sweeten (cf. the relatively slow rate of de-sweetening in the temperature transitions). This slow rate of sweetening is paralleled by a slow rise in the respiration along AB, a deduction not borne out by observation. In addition, this slow rise is affected by the recovery from stimulation, which would further reduce the rate of sweetening and flatten still more the already very flat respiration effect curve.

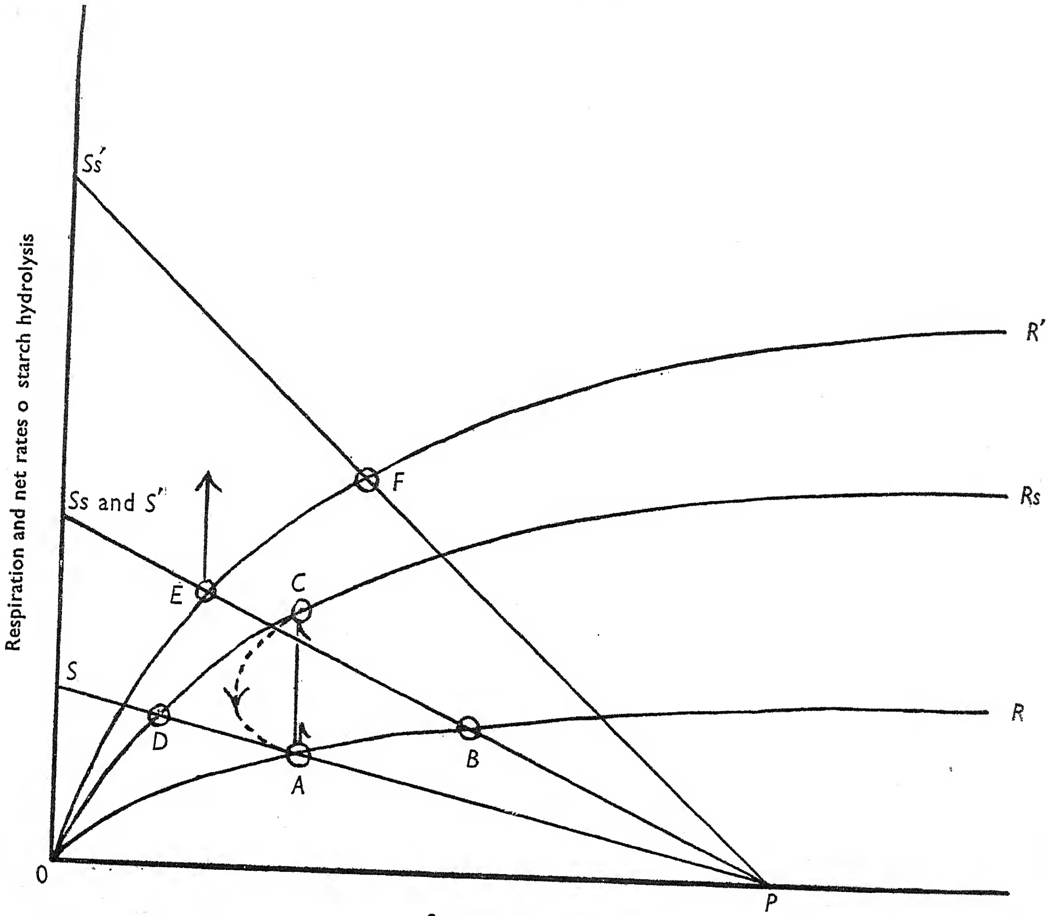

Fig. 6. Theoretical curves to illustrate the possible effect of stimulation on respiration and its relation to temperature (for explanation see text).

Similarly, curve $S'sP$ is the 100% stimulated hydrolysis curve for $T+10°$ C. At this temperature the respiration would tend to rise and fall slowly on stimulation along EF. Here another point is apparent. If the relative magnitude of the effect of stimulation on hydrolysis is the same at all temperatures, then the percentage rise of respiration should increase with temperature, a forecast not borne out by observation (Fig. 5). To explain the results we should therefore have to postulate impossibly large stimulations of hydrolysis rates at low temperatures.

What, on the other hand, would we expect if mechanical stimulation were affecting the respiration process itself, causing a sudden increase in the oxidative breakdown of sugar? Returning to Fig. 6, *ORs* represents the curve for the stimulated respiration at $T°$ C. (twice height of curve *OR* at all concentrations of sugar). Here the respiration rate would rise immediately on stimulation from *A* to *C*. If the respiratory system remained in this stimulated state the respiration and sugar concentration would fall along curve *CD* to the new sugar equilibrium value at *D*, giving a recovery curve rather reminiscent of the temperature transition curves themselves. The activity of the respiratory system will, however, return slowly to its normal unstimulated state. The respiration rate itself will fall rather more rapidly, as a result of these two factors, along some such curve as shown by the dotted line *CA*, until it reaches the original unstimulated sugar concentration at *A*. Here it will be noted that the percentage rise of respiration is independent of the sugar concentration, and therefore its constant value over the range of temperatures studied needs to explain it only a constant relative stimulation effect, which is independent of temperature.

Conclusions

The conclusions from the results of experiments at these four temperatures over a range of 30° C. are mostly drawn from evidence of an indirect nature. The data, however, do indicate that mechanical stimulation acts on that part of the total respiratory system concerned with the oxidative breakdown of sugars, and leaves the reserve (starch)$\rightleftharpoons$sugar balance unaffected, except in so far as it is altered by changes in sugar concentration brought about by changes in its rate of consumption in respiration. This is in accord with the previous results on stimulation in nitrogen (1940). The theories developed in this paper show how an increase in the activity of the enzymes controlling the oxidation of sugars can account for the observed respiratory effects.

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ECOTYPIC DIFFERENTIATION

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(With Plate 2 and 1 figure in the text)

CONTENTS

I. Introduction

All plants do not occupy their optimum habitats; nevertheless, it is true to say that 'it is the environment, the competition, etc., which determine the place of the species in nature'. In fact, tolerance to a range of environmental conditions is a specific attribute just as much as any taxonomic character. Thus, theoretically, we might consider describing a species or any other biological unit in terms of its local hereditary reaction to environment, that is to say in terms of the sum of its organic attributes which are demonstrably related to environment. This ideal is, however, beyond practical achievement, and we are forced, as Raunkiaer says, 'to content ourselves with characterizing life-forms by using an essential side of adaptation'.

The three principles laid down by Raunkiaer (1908) for the study of adaptational attributes, though formulated with reference to species, might equally well serve as working bases for the study of the eco-geographical pattern of hereditary variation at the infra-specific level. These principles are:

'(1) The character must in the first place be essential; it must represent something fundamental in the plant's relationship to climate [presumably in the widest possible sense of the word].

'(2) It must be fairly easy to use, so that we may easily see in nature to which life-form a plant belongs.

'(3) It must represent a single aspect of the plant, thus enabling a comparative statistical treatment of the vegetation of different regions.'

Taxonomic species were Raunkiaer's ultimate bio-geographical units, and while he held that vegetational characterizations, expressed in terms of life-forms, are better indicators of ecological communities than are floristic lists, his conclusions were, nevertheless, founded upon floristic data because it happened that the attributes chosen by him vary comparatively little within taxonomic species. By transferring the emphasis from

the taxonomic constitution of communities to their life-form characteristics, established on the basis of the amount and kind of protection afforded to the buds and shoot apices of individual species, he was able to describe the flora of an area in terms of the percentage frequency of these life-forms.

Whenever we apply Raunkiaer's principles to the distributional problems of intra-specific variation we enter the field of genecology, the field of population genetics. Genecology as originally explained by Turesson (1923, p. 173) is largely concerned with 'the grouping in nature of individuals into ecospecies and ecotypes, representing various combinations of Mendelian factors, and the causes controlling this grouping'. Thus genecology is mainly concerned with the study of intra-specific patterns, and since it is our aim to see how far these patterns are caused by or, at least, associated with, ascertainable environmental conditions, our first concern is to reduce the environment to the simplest possible terms. While in theory we are bound to appreciate Raunkiaer's point of view that all the factors necessary for plant life are of importance, inasmuch as the plant life cannot exist in the absence of any one of them, yet from the standpoint of practical environmental analysis we cannot but welcome his conclusion that 'it is not incorrect to say that some factors are more important than others'. Here then we find the basis for a practical subdivision of the environmental complex into its component gradients, e.g. climatic, edaphic and biotic, that is, into gradients which, despite their interrelationships, are likely to exert a strong individual influence on the distribution of ecotypic variation. For instance, the zonation of mountain vegetation and the zonation of the vegetations of coastal mud flats provide illustrations of the predominating influences of altitudinal (climatic) and edaphic gradients. While it is true that phyto-social gradients are commonly coincident with those of climate and soil, this is not invariably so, for the independent activities of animals, including man, are capable of creating biotic gradients which can be appreciated as such.

Similarly, we shall have to resolve the hereditary variational complex into its practical components, in other words into measurable characters or life-forms, whose variation can be followed along our chosen environmental gradients.

The data presented in the present paper have reference to the European diploid population of *Plantago maritima* L., and among the characters whose variation has been studied along certain more or less conspicuous edaphic gradients are plant size, growth habit and reproductive capacity.

Plant size. Various methods of assessing plant size have been tried, and by far the simplest and probably ecologically most instructive size index was obtained from the measurement of the longest scape after flowering had ceased (scape = leafless flower stalk proceeding from the stock: the scape measurements also included the inflorescence or spike). Scape length is positively correlated with leaf length; for example, the correlation between sample means in respect of these two characters for a series of thirty-seven British populations was $+0{\cdot}902$. On this account the value of scape length as an index of plant size is enhanced.

Growth habit. Growth habit varies continuously from decumbent to erect. The range was divided into five classes or grades (1 denoting decumbent, 5 erect habit), and recording was done by reference to type photographs (Gregor, 1930). There is close agreement between the data obtained in this way and from direct measurement of scape systems expressed as scape spread/height ratios.

Reproductive capacity. Flower number has been used as the index of reproductive capacity. For example, if the sum of a plant's spike lengths was 5000 mm. and an average spike measured 100 mm. and bore 110 flowers, then the index accorded that plant was 5500. Direct counting, except in the case of relatively small plants, was too laborious for general application, as large plants may have upwards of 40,000 flowers. At first sight the most obvious criterion of reproductive capacity is seed number. However, seed number is subject to serious error, for in the sea-plantain it is almost impossible to avoid loss of seed both before, and at the time of, collecting the spikes, and for this reason it was discarded in favour of flower number. Admittedly the flower index does, in certain circumstances, differ widely from one based on total seed output. Nevertheless, in view of the very high proportion of flowers that produce capsules under good cultural conditions, this flower index can be regarded as a reliable one so long as we are dealing with plants in the garden, or growing under favourable conditions in the wild.

II. BREEDING STRUCTURE

Since the differentiation of habitat population is not unconnected with breeding structure we cannot rightly pass on to the consideration of ecotypic differentiation, i.e. hereditary differentiation occasioned by the selective action of the habitat environment, without at least a brief reference to the breeding potentialities of the population as a whole.

In Britain *Plantago maritima* occurs most abundantly along the sea coast though it has numerous inland stations, especially in upland districts. Its coastal distribution is usually regarded as continuous, but this is true only in so far as the distance between local populations is generally considerably less than what can reasonably be said to be effective seed dispersal distance.

Discontinuity has been aptly defined by Cain (1944, p. 361) 'as a distance between organisms that is greater than the maximum chance for crossbreeding'. This takes into consideration gametic dispersal, and in the wind-pollinated sea-plaintain a spatial separation well within the dispersal limits of pollen is apparently sufficient to afford a degree of isolation which will allow communities to assume a genetic individuality of their own. In this connexion it is worth noting that the coastal distribution is essentially linear, and even inland populations tend to occur in a series of linear sequences near the margins of mountain streams.

Colonization is no doubt usually accomplished by the water dispersal of free seed, but among the aggregations marking the flood limits of mountain streams spikes wrapped in debris have been found. These accumulations effectively prevent normal seed fall and thus enable a number of seeds from a single plant to reach a new habitat simultaneously. This fortuitous sampling does not, however, end with the establishment of pre-adapted immigrants, for so long as the number of breeding individuals remains small the allelomorph frequencies are liable to change at random by the process of drift enunciated by Wright (1940). Therefore the numerically very small population is not ideal for the study of ecotypic differentiation.

Table 1 summarizes some data concerning the breeding strength of four isolated inland populations established within the past eighteen years. It will be noted from column 4 that only about half the total of plants in the respective populations were breeding in the year of examination, and from column 5 that about a quarter of these breeding individuals

supplied half the annual seed output. Thus the actual breeding assemblages are in effect even smaller than the numbers of breeding individuals suggest.

A small breeding total is, however, not always associated with such numerically weak populations. For example, in one coastal habitat covering roughly 200 sq.yd. there occurred an almost pure culture of non-flowering plants. In this case individuals could not be distinguished, but assuming the density to be not more than 15 per sq.yd., a conservative estimate, the total population would number something in the region of

Table 1. *The breeding structure of four colonizing populations*

Population	Total no. of plants	No. of breeding plants	% breeding plants	Least % breeding plants contributing 50 % of seeds	Seedlings		Total plant density per sq.yd.	
					No.	%	Mean	Minimum
I	208	86	41	21	7	3·4	4·2	29
II	86	38	44	20	28	32·6	3·6	18
III	36	18	50	22	15	41·7	1·4	16
IV	16	7	44	26	1	6·3	1·1	6

3000 individuals, of which only 16, or 0·5 %, contributed to the breeding population. Moreover, of these 16 plants 6 failed to develop seeds and the remainder, 0·3 % of the population, produced a total of only 25 viable seeds.

If we consider that in the colonization of habitats, even from a common source, initial contributions are liable to differ as a result of the migration of unrepresentative samples, and that during early colonial life random drift may be responsible for further local differences, it is only to be expected that populations occupying similar habitats will not be genotypically identical. Thus the ultimate achievements of selection are influenced by past events which complicate the ecotypic picture and call for caution in assigning ecotypic significance to population variation.

III. The pattern of ecotypic differentiation

For the purpose of examining the manner in which variation is distributed along environmental gradients we shall take as examples three ecological series of populations, each series being represented by three samples collected from different points on their respective gradients and grown from seed under the uniform environment of the experimental garden. Samples *a*, *b* and *c* of series I and II (Table 2) are Scottish in origin and respectively represent populations occupying equivalent points on similar edaphic gradients in the island of Lewis, and the Firth of Forth. In both these series sample *a* is typical of the populations occupying the waterlogged mud of the littoral zone, sample *c* of the fertile coastal meadows above the tide mark, and sample *b* of habitats approximately midway between these extremes. The soil of the extreme habitats was analysed by Dr A. M. Smith of the Edinburgh and East of Scotland College of Agriculture. The results showed that the content of soluble salts in the waterlogged soil was nearly ten times that of the meadow soil, and that the former contained chloride equivalent to 2·5 % NaCl for the air-dry soil. The samples *a*, *b* and *c* of series III are from south-western Iceland and respectively

represent populations occurring on the walls of a hot spring, in positions between springs, and in an adjoining pasture beyond the spring area.

Distribution of growth-habit variations. The data presented in Table 2 show that as the conditions for growth improve the proportions of the growth-habit type change and the higher grades, i.e. the more erect variates, increase in frequency at the expense of the lower grades. But even at the extremes of the edaphic gradients variational discontinuity is never achieved, and as far as growth habit is concerned the habitat populations overlap each other.

Table 2. *Series I, II and III. Frequencies and intergradation indices*

Sample	Mean scape length (cm.)	Growth-habit grades (percentages)					Inter-gradation index*
		1	2	3	4	5	
Lewis:							
I *a*	15·2 ± 0·43	83·9	10·3	5·8	—	—	
I *b*	25·4 ± 0·66	53·5	27·7	17·8	1·0	—	*ab* 35
I *c*	33·9 ± 0·45	8·0	22·0	62·0	8·0	—	*bc* 24
Forth:							*ac* 12
II *a*	23·0 ± 0·58	74·5	21·6	3·9	—	—	
II *b*	38·6 ± 0·57	10·8	20·6	66·7	2·0	—	*ab* 18
II *c*	48·9 ± 0·54	—	2·0	61·6	35·4	1·0	*bc* 33
S.W. Iceland:							*ac* 3
III *a*	13·2 ± 0·46	82·8	15·6	1·6	—	—	
III *b*	15·9 ± 0·92	81·5	11·1	7·4	—	—	*ab* 47
III *c*	23·0 ± 0·74	31·1	39·0	24·4	2·5	—	*bc* 25
							ac 24

* Represents the measure of the area of overlap of the two histograms expressed as a percentage of the sum of their two areas (Ginsberg, 1938, p. 259).

We see from Table 2 that with one exception all samples contain decumbent variates, that is, contain variates with the peripheral arrangement of scapes which characterizes grade I. But a glance at column 2 will show that as we ascend the edaphic scale plant size increases, which suggests a relationship between the increased incidence of the more erect variates and large plant size. This relationship is confirmed by a series of twelve habitat samples showing a correlation of +0·628, significant at the 5% level, between the means of scape length and habit grade. That these size differences involve the decumbent variates can be seen from Pl. 2 and the scape-length means given in Table 3. Moreover, there is a tendency for grade I plants to have a lower mean scape spread/scape height ratio, i.e. they are less decumbent, at the upper edaphic levels.

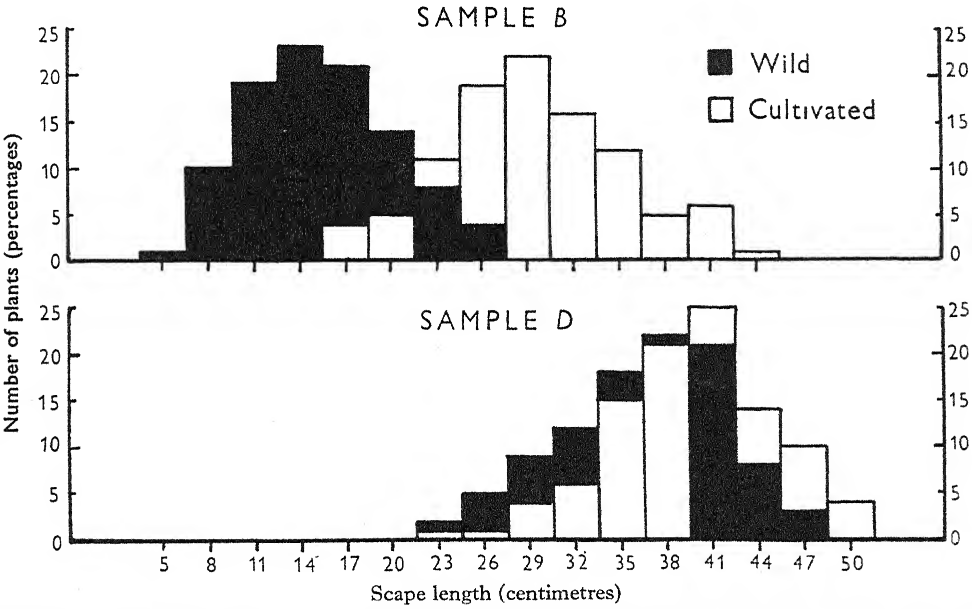
Table 3. *Hereditary changes in the expression of growth-habit grade I in samples a, b and c*

Series	Scape length (cm.) in samples			Scape height (in.)			Scape spread/scape height in samples		
	a	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
I	15·0	23·8	31·8	4·0	5·8	10·3	2·4	2·4	1·5
II	21·8	33·5	—	6·4	10·6	—	2·1	1·5	—
III	12·6	16·2	22·2	3·0	4·0	5·6	2·8	2·4	2·4

Since intra-ecospecific variation in growth habit is associated with the edaphic gradients under review, the habitat populations which differ in this respect are ecotypically

differentiated. It is, however, obvious that such differentiation is not accomplished solely by the elimination of unsuitable growth habits, but by a combination of elimination and size adjustment. Unquestionably it is the organism as a whole that is the adaptive unit, and in an endeavour to translate this idea into practical genecological analysis Sinskaja advocates the recognition of ecologically significant 'constitutions' or eco-elements. For instance, the variates included in our grade I she would regard as constituting a decumbent eco-element. As this eco-element, in common with members of the other grades in the growth-habit series, is not identical at the different edaphic levels owing to different expressions of size, the continuity of the habitat populations illustrated in Table 2 is not strictly speaking due to overlapping of growth-habit variation but, as Sinskaja would phrase it, to a spirally over-lapping series of eco-elements.

Reverting to Table 2 we find that the nearest approach to growth-habit discontinuity occurs between samples *a* and *c* of the Forth series (intergradation index is 3 %), whereas



Text-fig. 1. Scape-length frequency distributions. (Mean scape lengths in cm.: sample *B*, 'wild' 15·4 ± 0·48, cult. 29·4 ± 0·60; sample *D*, 'wild' 36·4 ± 0·54, cult. 39·6 ± 0·54.)

sample *a* from Lewis almost exactly coincides with sample *b* from Iceland (index 49 %). Since these two latter samples belong to different edaphic gradients their coincidence suggests the advisability of recording ecotypic character trends under titles indicative of the nature of the ecological gradients with which they are associated.

Since plant size is notoriously susceptible to modification it is of interest to compare the scape-length frequency distributions for both wild and cultivated material. In Text-fig. 1, sample *B* represents a breeding population of several thousands of individuals growing practically competition free in shallow rock fissures immediately above the tide mark, whereas sample *D* represents another numerically strong breeding population competing with a luxuriant growth of *Festuca rubra* in a fertile coastal meadow.

It is evident that the low fertility habitat does not provide the optimum growth conditions for its present occupants. However, despite what appears to be a selective pull

towards a still greater reduction in plant size, the data suggest that the population has reached a state of equilibrium. On the other hand, the meadow population shows little increase in plant size under garden conditions. In fact, it would seem that under the severe inter-specific competition in this biologically more advanced community, selection, in the form of a struggle for light, operates at or near the ceiling of production fixed by heredity, and that the size genes are being maintained at their present frequencies only under the stress of this selection.

IV. Growth habit, plant size and reproductive capacity

We have already seen that within climatic environments the proportion of erect variates increases as the soil conditions improve. The edaphic gradient, however, is associated with, and in fact occasions, a coincident phyto-social gradient which at the higher edaphic levels at any rate is likely to be selective. At these upper levels reproductive fitness is largely a matter of access to light.

However, before we proceed to discuss fitness under edaphic conditions favourable to growth we shall briefly examine the results of a 48-pot trial which involved hereditary large and small plants growing under four different soil treatments. While the same soil type was employed throughout, the treatments differed in the following respects:

Treatment	1	2	3	4
Surface area (sq.cm.)	298	298	123	123
Soil volume (c.c.)	3750	1875	900	450
Soil depth (cm.)	18·5	8·5	12·5	6·0

Although at the higher cultural levels flower number in the sea-plantain is regarded as a reliable index of reproductive capacity it is, as we shall see, by no means equally reliable under adverse growing conditions. Therefore in this trial, instead of assessing performance in terms of reproductive capacity, vegetative vigour was used, the criterion employed being plant weight, exclusive of scapes and roots. The seeds for the trial were obtained from a dwarf plant of habit grade II and from a tall plant of habit grade IV, which when growing as spaced plants in the experimental garden differed in scape length in the ratio of 1:2·6.

The decrease in plant weight from treatment 1 to treatment 4 in respect of the two plant types was of the following order: dwarf origin 100, 83, 67, 35; tall origin 100, 50, 49, 16. While the differences between treatments 1 and 2 and between 3 and 4 are for both plant types significant at the 5% level, the differences between treatments 2 and 3 are not statistically significant in either case. Now if we give the average weight of the dwarf plants at each soil level the value 100, then the relative values for the tall series are 110, 67, 80 and 50. There is therefore a 33% difference in favour of the small plants at treatment 2, whereas at treatment 3, with only half the volume of soil but with greater depth, the difference is reduced to 20%.

Tap-root development was decidedly less pronounced in the dwarf plants, and it is tempting to infer from this that where soil conditions are such as to prevent deep penetration of the tap-root small plantains are less likely to suffer loss of vigour than large ones.

Reproductive capacity in the absence of competition. In the first place we shall examine the interrelationships of growth-habit grade and flower number (i.e. the index of reproductive capacity), and of scape length (i.e. the index of plant size) and flower number both

within samples and within individual grades. The material supplying the relevant data was grown as spaced plants free of competition in the relatively high fertility soil of the experimental garden. The samples employed for these trials were collected from the Forth area and represent populations occupying positions towards the upper end of the edaphic scale.

There is a definite tendency within samples for reproductive capacity to increase as the plant becomes more erect as the following habit grade:flower number correlation coefficients show: +0·154 not significant; +0·368, +0·430 and +0·575 significant at the 1% level. Incidentally, Sinskaja's suggestion (1942) that within a breeding community the different growth habits may become isolated from each other owing to the non-

Table 4. *Scape length:flower number correlations within habit grades*

Sample	Habit grade	Correlations Sc. L.: Fl. no.	Sample means	
			Sc. L. (cm.)	Fl. no. (1000's)
1	I	—	36·0	9·0
	II	—	42·5	16·4
	III	+0·573	45·2	21·3
	IV	+0·546	48·9	21·0
	V	—	52·0	21·2
2	I	—	31·8	12·0
	II	+0·769	36·5	18·1
	III	+0·524	42·4	25·0
	IV	+0·632	43·0	25·3
	V	—	48·5	27·8

Coefficients are significant at the 1% level.

Table 5. *The correlation between plant height and flower number*

Sample	Correlation coefficients
5	+0·537
6	+0·295
7	+0·321
8	+0·276

All significant at the 1% level.

coincidence of their flowering times does not hold in these cases, for no significant correlations between habit grade and flowering time were obtained, the coefficients ranging from −0·181 to +0·164.

If we now turn to an examination of the reproductive capacity of variates of different sizes within each of the habit grades, we find that as plant size increases reproductive capacity again tends to increase (Table 4). This table also shows the sample means for scape length and for flower number in respect of the different habit grades.

In an advanced community it is tallness rather than actual bulk that brings a plant in reach of the light. Since the larger plants within a population are on the average erect they are commonly also tall. For a series of four samples the variation in scape height (the vertical distance from the ground level to the apex of the tallest spike) was grouped into six height classes (10–12, 13–15 and so on up to 25–27 in.), and these classes were correlated with their respective flower numbers. The results are given in Table 5.

Thus we see that within a population growing under conditions which favour reproduction erect plants of large size have a potential reproductive advantage on their own account, or, to express it another way, an advantage irrespective of any additional advantage which they might acquire if they were actually competing against the smaller decumbents.

Reproductive capacity under competitive conditions. In sparsely populated habitats reproductive capacity is little, if at all, influenced by competition, and consequently the available illumination is shared by large and small plantains alike. But wherever the community is dense, and particularly where the physical environment permits luxuriant growth, light becomes a selective factor of major importance. Any inherent gap between the reproductive capacities of small and large individuals is therefore likely to be widened under such competitive conditions. To put this possibility to the test a trial was designed wherein plants of different sizes were brought into competition with each other. Two groups of competing plantains were employed: (*a*) small diploids *v.* large tetraploids from a locality in the Alps, and (*b*) small *v.* large diploids from the Forth area. The replicated treatments were randomized in the customary manner, and the equal-sized plots were sufficiently separated to eliminate inter-plot competition. Eight treatments are relevant to the present inquiry, comprising (1) a central core of small alpine diploids surrounded by a ring of the same diploids, (2) a central core of large tetraploids surrounded by a ring of large tetraploids, (3) a central core of large tetraploids surrounded by a ring of small alpine diploids, (4) a central core of small alpine diploids surrounded by a ring of large tetraploids, and (1*a*), (2*a*), (3*a*) and (4*a*) in which Forth material replaced the alpine.

The results, which relate only to those plants occupying the peripheral rings, can be summarized as follows: compared with treatments (1) and (1*a*) the small plants in treatments (3) and (3*a*) showed respective reductions in flower numbers of 64%* and 24%†; on the other hand, the large plants in treatments (4) and (4*a*) showed increases of 62%* and 11% over treatments (2) and (2*a*). Thus not only was the reproductive capacity, as measured in flower numbers, of the small plants substantially reduced when in competition with the large plants, but that of the large competitors was, in one instance at least, significantly increased. If then a large plant has a reproductive advantage over a small one in the absence of competition this advantage is likely to be increased when the two types happen to be competitors under favourable growing conditions.

V. SEED SIZE AND REPRODUCTIVE CAPACITY

In the case of 33 northern European samples in culture, whose scape-length means ranged from $14{\cdot}0 \pm 0{\cdot}45$ to $52{\cdot}5 \pm 0{\cdot}67$ cm., the correlation between seed length and scape length was $+0{\cdot}720 \pm 0{\cdot}084$, while the corresponding coefficients for 15 samples from Britain alone was $+0{\cdot}825 \pm 0{\cdot}083$. This suggests an inherent tendency under garden conditions for the larger-sized plantains, and by inference, plantains growing in the more advanced communities, to bear the largest seeds.

The question now arises as to whether non-hereditary modifications in seed size affect the reproductive capacity of their generation. Table 6 gives data bearing upon this point, data which relate to the performance of seeds extracted from two-seeded capsules containing seeds of unequal size, and borne by plants of different hereditary size. These

* Denotes significance at the 1% level. † Denotes significance at the 5% level.

data indicate that the sea-plantain is no exception to the general rule that within a given hereditary category the initial advantage derived from a large seed is not reflected at maturity. However, this relationship, as might be expected, does not necessarily hold for seeds belonging to plants of different hereditary size. For instance, the plants raised from the small seeds (0·45 mg.) off the hereditary large plant II were compared with those raised from the large seeds (0·75 mg.) off the dwarf plant III. The plants from the smaller seeds not only had significantly (1 % level) longer scapes and higher flower numbers, but also larger seedlings on the average though not significantly so. Thus the ultimate performance of the products of large and small seeds of different heredity is not entirely a matter of initial food reserves.

On the other hand, the number of seeds produced per capsule and the proportion of flowers developing capsules has almost certainly a nutritional basis in normal diploid

Table 6. *Size and reproductive capacity of plantains raised from large and small seeds*

Parent plants ...	I	II	III
Large seed (mean in mg.)	1·41	1·28	0·74
Small seed	0·46	0·45	0·42
		Ratio: large/small	
Seed weight	3·07	2·84	1·76
Seedling length	1·63*	1·68*	1·30*
Scape length	1·18 NS	1·12 NS	1·08 NS
Flower no.	1·00 NS	1·13 NS	1·36 NS

NS not significant.

* Denotes that the actual recorded differences were significant at the 1 % level.

Table 7. *The influence of a deteriorating environment on reproductive capacity*

Spike	Length (mm.)	No. of flowers	No. of seeds	% fertility
1st	97	103	209	203
2nd	76	98	159	162
3rd	51	63	83	132
4th	90	105	49	45

plantains. In habitats at the upper edaphic levels, and in the experimental garden, the proportion of flowers setting seed is very high indeed, and in such environments the potential reproductive advantage of hereditary large plant size is likely to be realized to the full. At the lower edaphic levels, however, the situation is different, and the higher nutritional demands of the very large plants may well act to their disadvantage.

The following data relating to the reproductive performance of a profusely hand-pollinated completely self-compatible diploid plantain growing in the rapidly deteriorating environment of a small plot, are at least suggestive of what may occur at different edaphic levels in the wild. The first spike produced by this plant was allowed to flower, and after an interval of several days, during which time any spike approaching the flowering stage was removed, another spike was permitted to flower. This procedure was repeated until four spikes had matured, with the results shown in Table 7. Before the flowers and seeds on the 2nd and 4th spikes were counted the spikes were divided into three approximately equal parts. For the lower, middle and upper portions of the 2nd spike the fertility percentages were 200, 170 and 116%, and for the 4th spike 55, 40 and 27%. A feature

of this latter spike was the high frequency of aborted ovules and shrivelled unviable seeds which resulted in the almost entire absence of two-seeded capsules. From the standpoint of seed size it is of interest to note that neither between, nor within, spikes were more than very minor differences in average seed weight recorded.

Seed and seedling survival. We have seen that there is a tendency for large seeds to produce large seedlings, and this leads to speculation as to whether initial competitive advantage is maintained beyond the seedling stage. It has been pointed out by Salisbury that elimination in the cotyledonary and juvenile stages is very great, and that the few individuals which successfully survive these stages grow on to reproduce. The rarity of young plantains in established populations suggests that in this species also seedling mortality is very high. It is by no means unusual for a plantain growing in the wild to produce 700–1000 seeds. In the more extreme habitats, however, individual output is often small. For instance, seed counts in respect of the constituents of a mountain population gave $26{\cdot}6 \pm 3{\cdot}65$ as the average output per plant. But even at this low level, assuming the average life of the reproductive individual to be no more than 5 years (some plants have reproduced annually for upwards of 15 years in the experimental garden), the survival of only one seed in 133 is all that would be required by way of replacement.

The following observations provide some slight indication of the stage of development at which plantain elimination is most pronounced. Four plots were seeded in October 1937 with 750 viable seeds each. Two of these plots were examined in August 1938, the plants being removed from the soil and counted. One contained 265 living plants (one of which was flowering) and 106 dead, the other 313 living (one flowering) and 203 dead, giving, in terms of actual seedlings counted, survival values of 71 and 61 % respectively, or in terms of seeds sown 35 and 42 %. The remaining two plots were examined exactly a year later. Each contained 19 plants of which 5 were flowering in one plot and 4 in the other. Now if we assume that the original number of plants in each of these two plots was that of the average number appearing in the plots examined in the previous year, i.e. 444 plants, we find that within a period of two years 96 % of the plants had been eliminated before they had reached the reproductive stage, and of the survivors less than one-quarter were sexually mature. The average community density had been reduced from 1·5 to 0·06 plants per sq.cm. during the year. After transplanting, the 29 non-flowering plants all flowered successfully in the following year.

VI. Discussion

From a comparison of species belonging to the same genus and from an analysis of data obtained from a diverse collection of species, Salisbury (1942, p. 18) reached the conclusion that 'with increasing density of a plant community in respect to shade there is a marked tendency for the seed weight to be augmented'. If the variation in seed size in the sea-plantain is in any way typical of the state of affairs obtaining in other species, then this generalization is equally true of intra-specific variation.

Under competitive conditions there would seem to be no reason to doubt that initial success is potentially advantageous, but whether large seed size has in any way contributed to the attainment of the large plant size which we find in these advanced communities, or whether it is merely an inevitable accompaniment of the latter attribute, is by no means clear. It is perhaps worth recalling in this connexion that where seeds are of approximately the same weight those off hereditarily larger-sized plants tend to produce the most

'vigorous' seedlings. On the other hand, the most 'vigorous' seedlings are produced by the heaviest seeds when the differences in seed weight are modificatory.

Unfortunately, there are few data available which have a direct bearing on this important question of seedling mortality and survival. Salisbury's (1930) observations are therefore all the more valuable on this account. His figures show that in the annual species *Silene conica* L. 95 % of the population died as seedlings, and that in the biennial *Verbascum Thapsus* L. less than 0·1 % of plants survived the first six months.

In addition to high seedling mortality the number of zygotes which fail even to achieve the seedling stage must normally be very large indeed. Some idea of seed loss may be gained from data collected from a small plantain colony with the low plant density (including seedlings, but exclusive of the few scattered individuals belonging to other species) of 1·6 per sq.yd. The number of seedlings counted in the spring represented no more than 0·3 % of the following autumn's total seed output. Judging from the scarcity of plantain seedlings in more densely populated habitats establishment of seedlings must often be very considerably less than 3 per 1000 seeds.

Salisbury argues that the adult characters, apart from those concerned with pollination and seed dispersal, are subordinate to the juvenile in determining survival. Such wholesale destruction as the above figures suggest, however, savours more of fortuitous survival than of selection of the hereditarily fit. Differential seedling elimination is at a minimum when seed samples are cultivated for examination. Accordingly, the close correspondence between the size characteristics of samples raised from random seed collections, and those of plant samples directly transplanted from the wild, does not suggest that seedling mortality provides a measure of the elimination of hereditary misfits. Within a habitat, opportunities for seedling establishment vary very considerably, and it is not unreasonable to assume that the seedling which happens to find itself favourably situated has a greater expectation of survival than one of similar constitution less fortunately placed. But even if seedling survival is largely dependent on selection it would certainly be a mistake to underrate the part played by the physiological characteristics, if not the morphological, of established individuals in determining which variates shall contribute more than their share to the next generation in a given habitat (cf. Lawrence, 1945, figs. 7 and 8).

Incidentally, the elimination of zygotes as seeds or seedlings is as nothing compared with the loss of gametes in the form of pollen. For instance, Cranwell (1939) states 'that it has been estimated that *Alnus glutinosa* yields about four million grains per catkin, and that during a dust storm in 1934 oak pollen fell at the rate of 3·4 tons per square mile, as measured at Chicago by the exposed slide technique' (Cain, 1944, p. 137).

Salisbury's generalization still holds good, if to seed size we add hereditary plant size and reproductive capacity, for plantains tend to be larger and taller, and to have a higher reproductive potential at the more advanced stages of plant succession.

At the lower edaphic levels, and hence at the less advanced phyto-social levels, one of the most striking features of the plantain populations is the prevalence of decumbent variates. Why this should be is not self-evident, though it is possible that among small plants the reproductive capacity of decumbents is least affected by deficient nutrition. It does not follow, however, that these decumbents grow best under such conditions, in fact they grow very much better under cultivation. All that can be said is that under adverse conditions they apparently have a higher survival value than their competitors.

On the other hand, decumbent plants also occur, though in much diminished frequency at the other end of the edaphic gradient, but they are now of greater hereditary size. Thus while the decumbent plant still persists in the advanced community it has changed its form to one that is more in keeping with the needs of a plant forced to compete with a tall vegetation. The ecotypic process is, therefore, constructive at the same time as it is destructive, putting a premium on progress towards greater fitness while discarding the less fortunate variates which fail to reach the requisite standard. Each 'improvement' in the environment occasions an ecotypic shift until a point is reached beyond which ecotypic response cannot go and the species is ultimately excluded from the community.

In the study of ecotypic differentiation the question of what should constitute the sampling unit is a primary one, and the answer to this question very largely depends on the breeding structure of the species concerned. The distributional pattern of a regional plantain population is perhaps best regarded as a loosely co-ordinated syngameon of considerable ecological potentiality comprising numerous more or less isolated breeding colonies or gamodemes (Gilmour & Gregor, 1939) which are commonly recognizably different though not necessarily ecotypically distinct. This colonial structure is a result of the spatial continuity of congenial habitats being much interrupted, the intervening uncongenial areas being either devoid of plantains, or relatively thinly populated.

As a general rule, though by no means without exceptions, the nearer a plantain population approaches a pure culture the greater is the number of breeding individuals per unit area. This is a relevant point, for although the likelihood of obtaining a truly panmictic population is increased when the colonial area is small, it is essential that the numerical strength of the breeding constituents be duly considered. Judging by the degree of ecotypic differentiation exhibited by the partially isolated populations of the Lewis, Forth and Icelandic series we may conclude that in so far as selection for growth habit and plant size was concerned, with breeding strength estimated at something between 5000 and 10,000 individuals, ecotypic selection has been more effective than random drift in determining the direction of change. In view of the peculiarities of species it is obviously impossible to suggest any standard for the sampling unit, but the ideal of the partially isolated gamodeme comprising upwards of a thousand breeding individuals has been regarded as a suitable working hypothesis when in search of plantain samples.

It is not uncommon to find populations occurring at what is apparently the same ecological level on a particular environmental gradient, exhibiting ecotypically anomalous variation. However, it is often possible to throw an erratic trend into bolder relief by grouping the data from colonial samples collected at approximately the same environmental level. An extreme example of anomalous differentiation on a climatic gradient is mentioned by Sinskaja (1931, p. 66), where a local phyto-social environment was found 'to direct selection along quite an opposite line' to that of climate. Now if we refer back to Table 2 we find that the trend of variation in the series of samples from Lewis is paralleled in the Forth series, but we also find that the mean plant size of each Lewis sample is less than that of its Forth counterpart. Though it is possible that the Lewis habitats chosen for sampling are consistently lower on the edaphic scale, it is equally possible that we are here dealing with an edaphic gradient which makes its appearance at different points on an, as yet, undetermined climatic gradient. Be that as it may, the fact remains that the edaphic trend still remains recognizable as such.

There is a considerable amount of truth in saying that 'we seek simplification through

classification of ecotypes and other biological units, only to discover that thereby we have multiplied the complexity' (Lawrence, 1945, p. 312). The intensive study of intra-specific variation undoubtedly creates its own classificatory difficulties, some of which have already been discussed in a previous paper (Gregor, 1944), and more recently by Turrill (1946). However, at the moment the main point at issue is whether in actual practice it is customary to delimit ecotypes with reference to the general conditions of their habitats, or to particular environmental gradients. While it is often implied that an ecotype is described in terms of its response to total environment, the fact that climatic and edaphic ecotypes are recognized by Turesson, climatic ecotypes by Clausen, Keck & Hiesey and by Lawrence, and climatic, edaphic and phyto-social ecotypes by Sinskaja, at least suggests that the environmental gradient of major effect is widely accepted as being the most convenient ecological background to the study of ecotypic variation.

It should perhaps be emphasized that the ecotype concept (Turesson, 1922) embraces all intra-ecospecific variation of ecological significance, the term 'ecotype' being applicable to any population differentiated in respect of any characteristic attributable to the selective action of ecological factors. It is therefore highly probable that the majority of taxonomic subspecies and varieties will on experimental examination be found to bear ecotypic characteristics.

While ecotypic subspecies and some ecotypic varieties represent relatively well-defined areal assemblages, the characteristics of an ecotypic trend may happen to include the diagnostic features of a number of less well-differentiated taxonomic units. For instance, Böcher (1943) has shown that in *Plantago lanceolata* L. most of the taxonomic varieties and subvarieties correspond to ranges of ecotypic variation. This is because taxonomists happen to have described their varieties in terms of a character which exhibits an ecotypic trend. The same is true to some extent on *P. maritima*. In the case of *Veronica officinalis* L. on the other hand, taxonomists have avoided the ecotypically significant character leaf size (Böcher, 1944). The result is that, whereas in *Plantago lanceolata* and *P. maritima* certain ranges of ecotypic variation in growth habit do correspond to varieties, in *Veronica officinalis* there are no equivalent varieties in the leaf-size ecotypic trend.

The fact that the orthodox taxonomic system makes no provision for recording physiologically differentiated but morphologically similar units is an unfortunate, though understandable, weakness from the standpoint of ecology. That is not to say that when delimiting his morphological units the taxonomist ignores physiological criteria, but only that physiological attributes do not receive taxonomic recognition on their own account. Thus a physiologic ecotypic trend would not be amenable to taxonomic treatment so long as it lacked reference to morphological variation. In this connexion it is of interest to note that Clausen *et al.* (1940) have divided the subspecies *nevadensis* of *Potentilla glandulosa* into two physiologic ecotypes, a subalpine and an alpine. Since these ecotypes represent what are apparently arbitrary subdivisions of a range of ecotypic variation, we have here a precedent for applying the term ecotype not only to an ecotypic range but to a range which in the circumstances cannot receive taxonomic recognition. Similarly, the ecotypes of *Deschampsia caepitosa* (L.) Beauv. described by Lawrence (1945) cannot be morphologically distinguished, and must, as he says, remain for the present as experimental categories only.

Huxley (1939, pp. 491–2) has pointed out that 'while it is known that many organisms

vary geographically and ecologically in a graded way no recognized terminology exists for these gradients. This is unfortunate for several reasons: (*a*) When gradation exists within a group, the mere conferring of a subspecific or a specific name gives a false impression of the geographical homogeneity of the group. (*b*) When intergroup gradation exists, mere naming and description of the separate groups not only does nothing to bring out the gradation in their characters, though this relation of connexion may be at least as important as their separation with regard to difference of characters, but it may even serve to disguise it. Finally, when an intergroup character gradient comprises some named (subspecific) group and others which are unnamed, this disguises the fact that all groups are of equal importance in regard to the relation of connexion. A name confers a false sense of importance on a named group.'

It is only necessary to read Druce's (1920) account of the taxonomy of the sea-plantains of Britain to appreciate how valid is Huxley's criticism.

To satisfy the need for a recognized system of recording graded variation in such a way as to give expression to this relationship of connexion, Huxley (1938) introduced the now familiar cline terminology. The ecotypic trends which we have been discussing are clines or to be more precise *ecoclines*.

Ecoclinal variation bearing some resemblance, in so far as plant size is concerned, to that found in *Plantago maritima* has been described in *Viola Riviniana* by Valentine (1941). This ecocline is related to a sheltered woodland—semi-sheltered long grass—exposed short turf environmental gradient, and comprises subsp. *nemorosa* (large size)—forma *intermedia* (intermediate size)—subsp. *minor* (small size). An interesting feature is the way such ecoclinal variation is geographically distributed; for instance, in parts of eastern England, where apparently suitable *minor* habitats exist, only the *nemorosa* range occurs, whereas westwards in Wales the complete range is found.

The existence of ecoclines can, however, only be proved where variation is shown to follow environmental gradients. Thus even if we were to assume a current ecological value for all characters, the chances of assigning ecoclinal significance to all variational trends would indeed be slight in view of the practical difficulty of analysing the details of the environmental complex. It is little wonder, therefore, that there is likely to remain a very substantial residue of *topoclines* (Gregor, 1939), that is, of character trends of doubtful ecological relationship or of no apparent ecological significance whatsoever. It may even happen that the same character varies topoclinally as well as ecoclinally. For instance, Böcher (1944) has shown that leaf size in *Veronica officinalis* increases 'as one moves northwards and eastwards in Europe away from the most oceanic regions' (p. 15), and as no definite ecological relationship has been established for this trend he very rightly suggests that this leaf-size variation forms a topocline. But since leaf size varies ecotypically when followed from woods out into the open, he is of the opinion that leaf-size variation also forms an ecocline. On the other hand, so far as hairiness is concerned the species forms a topocline only, the glabrous types occurring principally in the north-west of Europe.

Just as particular ranges of ecoclinal variation have been called ecotypes, so topoclinal ranges of note have been referred to as *topotypes* (Gregor, 1939, p. 319), and, as in the case of ecoclines, topoclinal ranges may correspond to taxonomic units.

The difference between the infra-specific taxonomic categories, and the eco- and topotypes is, however, often fundamental, for whereas taxonomic treatment aims at emphasizing variational discontinuities, the experimental treatment endeavours to give expression to

variational streams and trends of character combination. For instance, *Plantago maritima* var. *punctata* (Neuman, 1905, p. 256) can be discontinuously delimited on account of its spotted leaves. The difference between this variety and non-spotted plants is dependent on a single gene, and the continuous geographic variation in the proportions of the two variates is topoclinal, e.g. populations of the arctic topotype contain on the average a higher proportion of spotted individuals than do those of the British Isles topotype. Thus the bio-geographical interest of the spotted condition is not simply a matter of the distribution of var. *punctata*, i.e. of a discontinuous variate class, but centres on the distribution of the variation in the proportions of the two contrasting classes.

This problem of how to analyse and classify infra-specific variation is becoming increasingly important in relation to ecological and bio-geographical studies. It is only now being appreciated that specific tolerance to environment, and hence specific distributional potentiality, rests on the ecotypic composition of species, a composition which finds expression in the ecocline. That is not to say that the apparently non-adaptive topocline is of any less bio-geographic consequence; perhaps of the two the topocline is intrinsically more interesting, as some topoclines doubtless reflect old variational patterns upon which have been superimposed the ecoclines of to-day.

VII. Summary

1. While the floristic compositions of communities change at different points on an environmental gradient, so ecotypic changes take place within the prevailing species until a point is reached beyond which selection cannot go for want of material and the species is ultimately excluded from the community. This process is illustrated by the shift in the ecotypic composition of sea-plantain populations as environmental conditions 'improve' on a soil gradient, the plants becoming hereditarily larger and taller, and having larger seeds and a higher reproductive potential at the more advanced stages of plant succession. The range of environmental tolerance of a species is therefore largely dependent on its ability to respond ecotypically.

2. Despite high juvenile mortality the characteristics of established individuals apparently play an effective part in determining which variates shall contribute more than their share to the next generation in a given habitat.

3. Though some degree of variational discontinuity may separate certain ecotypic ranges of variation, available evidence suggests that ecotypic differentiation is more often continuous than discontinuous. Continuously graded variation, especially when it involves physiological characteristics, is peculiarly difficult, if not impossible, to classify along orthodox taxonomic lines. It is, however, possible by recording ecotypic variation under ecoclines related to particular environmental gradients not only to present the variational picture in proper sequence but to relate variation to habitat conditions. As a matter of practical convenience it may be necessary to recognize as *ecotypes* particular ranges of ecoclinal variation and to give these ecotypes distinguishing names. Sometimes ecotypes bear the diagnostic characters of taxonomic units.

4. Where the spatial distribution of an ecospecific population is colonial rather than strictly continuous the partial isolation of habitat communities doubtless facilitates ecotypic differentiation.

5. Populations occupying what appear to be similar habitats are seldom identical, and where the breeding colony or gamodeme is employed as the unit of sampling it is not surprising that ecoclines are often irregularly regular.

6. A variational trend of geographical significance but for which no ecological explanation is apparent can be recorded under the title of topocline. It is possible for a character to vary topoclinally as well as ecoclinally.

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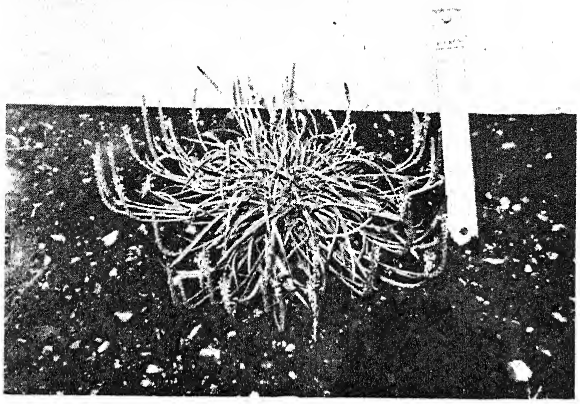
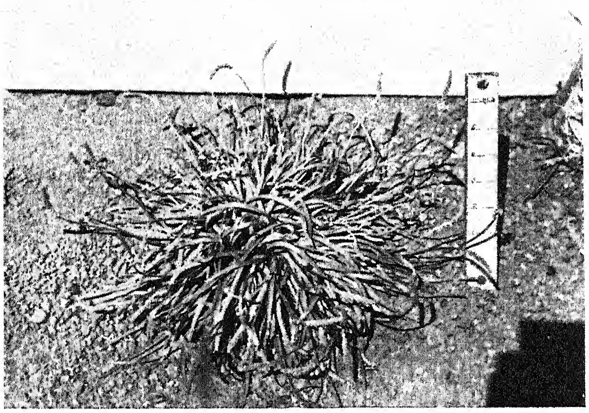
EXPLANATION OF PLATE 2

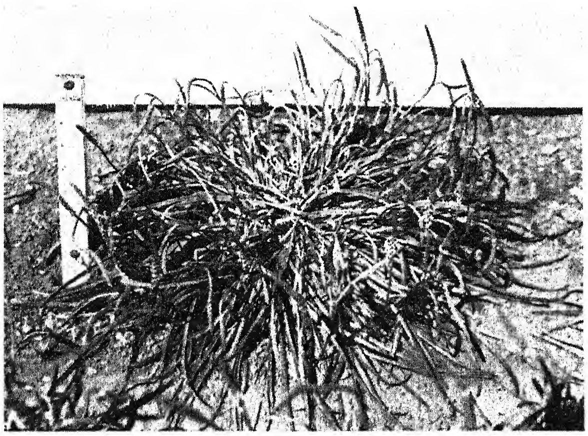
Hereditary differences in the size of the grade 1, decumbent, growth-habit variates occurring in the edaphically different habitat categories *a*, *b* and *c* (see Table 3).



a



b



c

GREGOR—ECOTYPIC DIFFERENTIATION

STUDIES IN ATMOSPHERIC POLLEN III.

POLLEN PRODUCTION AND POLLEN INCIDENCE IN RIBWORT PLANTAIN (*PLANTAGO LANCEOLATA* L.)

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(With Plate 3 and 1 figure in the text)

CONTENTS

I. Introduction. Site and situation

The pollen of Ribwort Plantain (*Plantago lanceolata* L.) is of interest both in relation to peat studies and to allergy: Iversen (1941) and Godwin (1944) have both used it as an index of the influence of prehistoric man on vegetation; while medical allergists in both Europe and America (Bray, 1937; Wodehouse, 1945) regard it as a more or less important cause of hay fever. The plant is of interest also for its own sake, as belonging to a predominantly anemophilous family which retains obvious vestiges of entomophily (Pohl, 1930). For all these reasons a study of pollen production and pollen incidence in this species would seem to be desirable. The results of such a study are set out below.

The observations to be described were made mainly on a population of Ribwort Plantain situated on the as yet unbuilt-on portion of the site of the National Museum of Wales (Plate 3), at about 45 ft. altitude near the middle of the city of Cardiff. This area was considerably disturbed by building operations between 1914 and 1931, after which it was levelled and allowed to become colonized naturally. Little soil properly so-called is present, the surface layers containing much Portland stone dust; for several years the vegetation has been mown once a year. The site is sheltered from the east and south but not overshadowed by buildings. The population concerned was concentrated mainly in an area 20 × 20 yd. (18 × 18 m.) but scattered plants also occurred on the adjoining parts of the site, i.e. within an area of approximately 65 × 40 yd. (60 × 36 m.). The surrounding streets and grounds were relatively free from the weed. At the relevant period (late April to early May 1945) the plantain was the most prominent feature of the vegetation (see photograph A, Plate 3). Later on, grasses and other herbs occupied most of the ground. The following species were noted during May:

Arrhenatherum elatius	a.	*Potentilla reptans*	o.
Poa pratensis	a.	*Tragopogon minus*	o.
Trisetum flavescens	a.	*Trifolium dubium*	a.
Bellis perennis	o.	*T. pratense*	o.
Crepis taraxacifolia	o.	*Rumex Acetosa*	r.
Hypericum perforatum	o.	*Vicia sativa*	o.

II. ANTHESIS AND POLLEN LIBERATION

Plantago lanceolata L. is very variable in respect of the size of the plant, the hairiness of its parts and the shape of the inflorescence. Typical specimens from the population here mainly concerned (Photograph B) appear to fall under var. *communis* Schlecht α subvar. *genuina* (Dietrich) Pilger as described by Pilger (1937), except that the bracts are no longer than the calyces. They agree, so far as Delpino's account allows one to judge (Delpino, 1870), with the form described by him as growing in meadows, tall (our plants had scapes measuring 22–58 cm.; arithmetic mean of 63 = 40 ($\pm$ 1 cm.)) and having broad white anthers which quiver in the wind. They have the white heart-shaped anthers referred to by Ludwig (1879) as being distinctive of one of the two forms described by him. They also agree with Müller's tall form 'from manured alluvial meadows' (Müller, 1883) described by him as having a scape 12–18 in. (30–45 cm.) long, with stamens projecting 6–7 mm. from the flower. A few plants identified as var. *anthoviridis* Wats. also occurred on outlying parts of the Museum site. Gynomonoecism, which is said to occur in this species, was not observed.

The flowers of typical *Plantago lanceolata* are functionally hermaphrodite and protogynous. The process of anthesis has been described from the angle of pollination by H. Müller. The following account incorporates also our own observations: 'While the lobes of the corolla are still erect, contiguous and covered by the sepals...the stigma [becomes] mature and protrudes more than 1 mm. beyond the bud' (Müller, 1883, p. 505). This phase (*a*) may extend over several days, during which the flower continues to grow in size: in particular the filaments elongate and become curved over into the shape of an inverted J. Toward the end of this period the corolla gapes open somewhat, displaying the apices of the anthers inside (phase *b*). Under favourable conditions the flower passes at the appropriate time of day (usually the early morning, see p. 274 below) into the male stage of anthesis (phase *c*). The lobes of the corolla fold back, the filaments rapidly elongate and straighten out, and the anthers become versatile and dehisce. Should unfavourable conditions supervene, however, when the flower has arrived at phase *b*, the flower may remain halted at that phase for several days.

In order to determine the mode of dehiscence and the speed of pollen liberation, various flowers were marked and their stamens removed at intervals one by one, beginning as soon as possible after anthesis was complete, transferred immediately to adhesive slides, mounted and examined. It was found that, under warm dry conditions in the middle of the morning, dehiscence may follow within 5 min. of the straightening of the filaments (though in other circumstances it may be delayed considerably; see p. 274 below). Each pollen sac dehisces by a longitudinal slit extending from end to end. The two sacs of one anther dehisce, if not simultaneously, within a few minutes of each other, and the four anthers of one flower all dehisce as a rule about the same time. Pollen liberation at the outset may take place along the whole length of the slit, or may at first be confined to one half or the other: given a gentle breeze, the great bulk of the pollen is shed within a few minutes of dehiscence; the residue (amounting to 4% of the original content at most), which may be distributed more or less throughout the sac (though more often than not some is retained in a little pocket at the apex) is shaken out much more gradually, and 0·5–1% may still remain even after 3 hr.

After the pollen has been shed the filaments remain turgid for some hours, but by next morning they have collapsed and the empty anthers have begun to wither and turn brown.

III. Pollen productivity

In order to determine roughly the rate of pollen production in the area concerned, counts were made of the numbers of grains liberated from groups of anthers, and also of the number of heads in flower per unit area and of the numbers of flowers observed per head on a 'good' day.

(i) The anthers of freshly opened flowers were removed before dehiscence and placed in stoppered tubes. After they had dehisced, the anthers in each tube were shaken up with a measured volume (2 ml.) of 50% methylated spirit containing fuchsin as a stain, until a uniform suspension had been obtained. The average number of grains contained in 1 cu.mm. of the suspension was determined from a series of counts made by the aid of a haemacytometer, and hence the number liberated by the anthers originally taken. The anthers were afterwards mounted, the relatively small number of grains remaining therein counted, and the necessary correction applied. Nine determinations were made in all, on batches of anthers ranging from 4 to 12. The number of grains per anther varied from between 15,700 and 29,500, the weighted average being 20,500 ($\pm$2200).

(ii) At midday on 6 May forty heads were collected at random from as many different plants growing within a few yards of the pollen-collecting apparatus (see below, p. 274). The lengths of the heads were measured and the number of freshly opened flowers on each was immediately counted. Spike length varied from 1·3 to 4·0 cm. and number of flowers from 3 to 36, the average being 11 ($\pm$1). Immediately after the end of the pollen catching experiment, ten 1 m. quadrats were set out at random within a distance of 4 m. of the apparatus and all plantain heads then in flower contained therein were collected and counted. The counts varied from 3 to 95 per m.^{2}, the average being 47 ($\pm$9). The average number of flowers which opened per m.^{2} on 6 May may be taken as $11 \times 47 = 517$, and the average pollen production therefrom, during the 24 hr. flowering period concerned, as approximately $517 \times 20{,}500 \times 4 = 42{\cdot}4 \times 10^6$.

IV. Flowering in relation to weather conditions

Plantago lanceolata (Photograph B) was observed at the male stage of flowering on 17 April; when the pollen catching experiment was started, eight days later, flowering had become general on the site and its progress was followed in detail for the whole of the following fortnight. As it was impracticable to watch continuously the actual plants at the National Museum, supplementary observations were made at two similar sites both within 3½ miles of the Museum. Whenever the three sets of observations were cross-checked they were always found to be in substantial agreement. In what follows, the results of these observations are described in relation to the weather experienced.* The estimated flowering intensity and the concurrent weather observations are set out diagrammatically at the foot of Text-fig. 1.

(*a*) *Temperature.* Favourable weather with warm days had been experienced between 17 and 25 April, but thereafter the temperature fell until on 30 April the diurnal range was from 29 to 47° F. Flowering declined correspondingly day by day, and by 30 April it had

* We have depended for the most part on weather records obtained at Penylan Observatory, Cardiff, and supplied by the courtesy of the City of Cardiff Public Health Department. The Observatory is situated at 202 ft. altitude about 1½ miles (2·4 km.) from the Museum.

become only slight. Temperatures remained low and the amount of flowering even smaller (though it did not cease completely) until 4 May; on this day the temperature range (35–52° F.) was almost identical with that experienced on 28 April at the beginning of the cold spell, though the amount of flowering was observed to be much less. (The great majority of the plants affected remained during the period 29 April–4 May in a stationary condition. Flowers which had attained the half open stage, with their anthers just showing (phase *b*, p. 272), remained thus—apparently on the point of completing anthesis—for several days, and only went on when the temperature rose sufficiently: for many plants this was on 6 May. Some inflorescences hung their heads in consequence of the frost but flowered in that attitude later.) With a further rise of temperature on 5 and more particularly on 6 May flowering reasserted itself and remained profuse until the last day of the experiment (10 May) when a distinct falling off was recorded.

(*b*) *Bright sunshine.* Profuse flowering took place on 26 April, 7 and 8 May before any bright sunshine had been registered on those days. On the other hand, several hours' bright sunshine on the mornings of 30 April and 1 May were followed by only slight flowering. Sunny days on 29 and 30 April respectively were followed by only slight flowering on the day after.

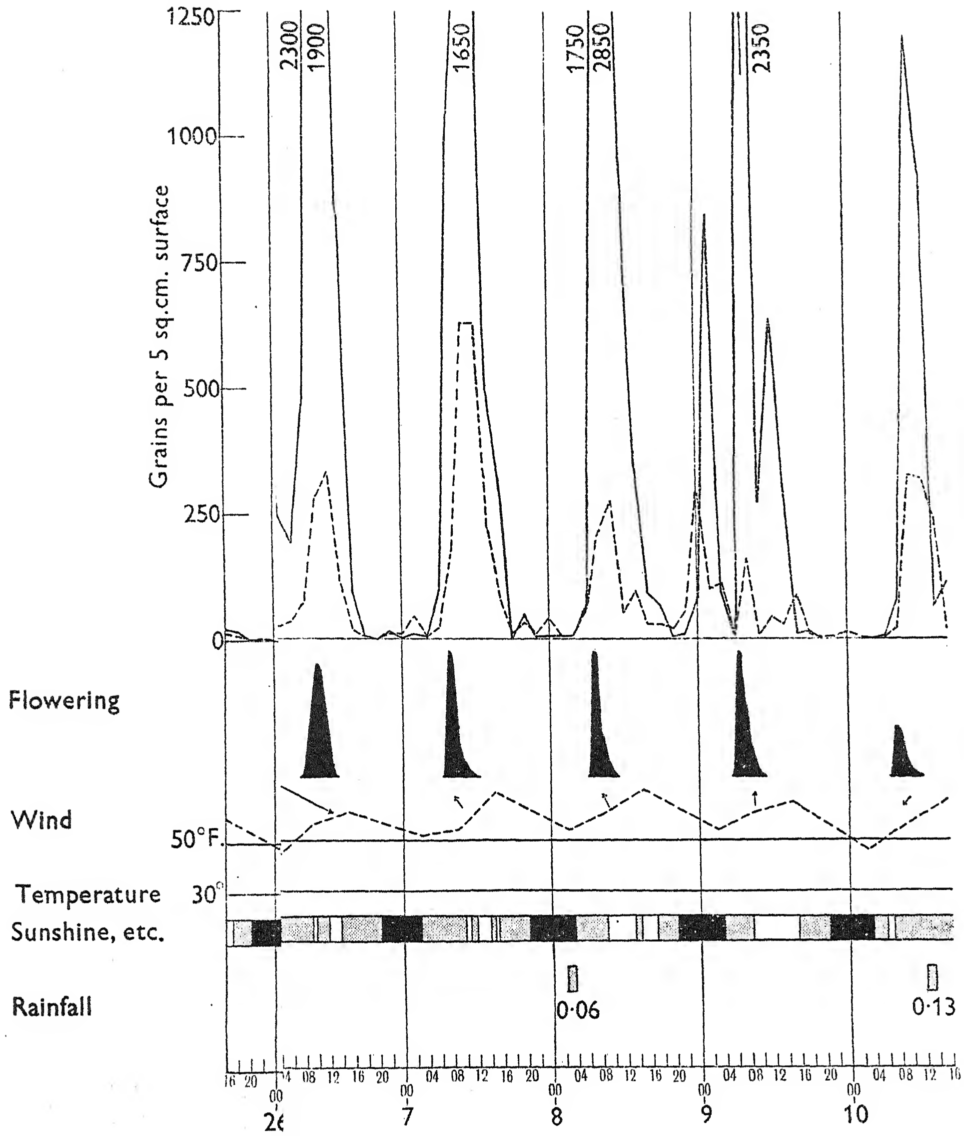
(*c*) *Rainfall and humidity.* Flowers were observed to be opening in spite of rain on 5 May. High humidity (80% saturation, or more) was recorded also on 6, 7 and 8 May: it was accompanied by profuse flowering on each of these days. On the last two dates delayed dehiscence was noted.

(*d*) The wind observations at Penylan Observatory were made some three hours later than the normal time of flowering. They show that except on 6 May (when a wind strength of 4 on the Beaufort Scale was entered) the wind on the mornings concerned varied from a light air to a gentle breeze. Additional observations made by ourselves showed that on certain occasions there was even less wind earlier in the day: thus, at 07.15 and 07.30 hr. on 8 and 9 May respectively, anthers which had dehisced remained stationary, and their pollen unshed, owing to the stillness of the air.

To sum up under this heading: male anthesis takes place normally at or before 06.00 hr.; dehiscence of anthers and liberation of pollen follow soon after, unless delayed by high humidity or absence of wind respectively; and flowering is virtually over by noon if not before. These processes took place substantially as described on eight out of the fourteen days of the experiment. They were almost entirely suspended on the remaining six days (which fell in the middle of the period) in consequence of a severe fall in temperature. It was noted that when the temperature at about 06.00 hr. was below 45° F. but rose above it a few hours later flowering was delayed and went on longer, but that the total amount was reduced. So long as the temperature remained below 50° flowering was almost completely suppressed; though, even on the coldest days experienced during the experiment, a few plants were observed in flower. No correlation was observed between bright sunshine and flowering.

V. Pollen incidence in relation to flowering

The pollen catching experiments were carried out in essentially the same way as those previously described on grass pollen (Hyde & Williams, 1945). Two slides were exposed in the middle of the plot of vegetation dominated by the plantain, both slides being contained in the one apparatus: one (the 'impact' slide) was held vertically in a metal



Text-fi of *Plantago lanceolata* 25 April to 10 May 1945. The continuous line stands recorded at 09·00 hr. at Cardiff (arrows point in direction of wind movem, (*b*) minimum, attributed to 03.00 hr., (*c*) maximum, attributed to 15.00 ation see text.

clip which was attached to one end of a metal bar which carried a wind vane at the opposite end and was pivoted centrally so that it moved freely bringing the slide to face into the wind. The other (the 'gravity' slide) rested on the lower of the two horizontal disks. The impact slide therefore stood at an average height of $17\frac{1}{2}$ in. (45 cm.), and the gravity slide lay 13 in. (31 cm.) above ground, as compared with 16 in. (40 cm.) the average height of the plantain inflorescences. These two slides were changed 2-hourly throughout the experiment, i.e. from 14.00 hr. on 25 April until 20.00 hr. on 10 May. A gravity slide was exposed in a similar apparatus on the roof of the Museum 60 ft. (18 m.) above ground and 78 ft. (24 m.) away measured horizontally (air distance, 100 ft. = 30 m.); this slide was changed every 24 hr. at 08.00 hr. It was not thought necessary to expose 2-hourly impact and gravity slides on the roof as was done for grasses in 1943 and 1944. The 'roof' slide merely served to record, however inexactly, the general trend of the changes in plantain pollen concentration in the neighbourhood.

The three series of slides were analysed for plantain pollen and non-plantain pollens only. The results of the analyses of the slides exposed in the apparatus on the ground are set out graphically in the upper part of Text-fig. 1. reference to which shows that except on two occasions (referred to below) the plantain-pollen catch varied from one period to the next exactly as the observations on flowering would lead one to expect.

Under favourable conditions the catch, after being negligible during the night hours, rose very suddenly and steeply between 06.00 and 08.00 hr. or 08.00 and 10.00 hr. and thereafter fell more or less steeply. The lag which was sometimes observed between time of maximum flowering and that of highest catch could be related, as stated, to calm conditions and consequent delayed liberation of pollen. The greater lag in the fall toward an approximately zero catch was evidently due in part to the liberation of the residual grains remaining in the anthers after the bulk had been shed. The effect of rain on the catch is evident on various dates, e.g. on 28 April from 18.00 hr. onward, on 3 May during the day, and on 5 May after 10.00 hr. The exceptional occasions when the pollen catch did not agree with expectations were between 00.00 and 06.00 hr on 6 and 9 May respectively, when a marked rise took place in both impact and gravity catch. It is difficult to account for this except on the assumption that on each of these two days an unobserved burst of flowering took place during the small hours.

The 'roof' catch is referred to below (p. 276).

VI. Discussion and conclusions

(a) *Pollen liberation and dispersal in ribwort plantain*

The results of the investigation confirm the conclusion previously arrived at by us that, in the middle of a stand of a herbaceous plant, the catch on an impact slide exposed at the appropriate height is a more sensitive index of rate of pollen liberation than is that on a gravity slide. It is seen further that in plantain, as in grasses, pollen liberation takes place during a definite period each day, while between times little or no pollen is set free. This latter conclusion is completely borne out by the field observations and by the examination of anthers in the laboratory.

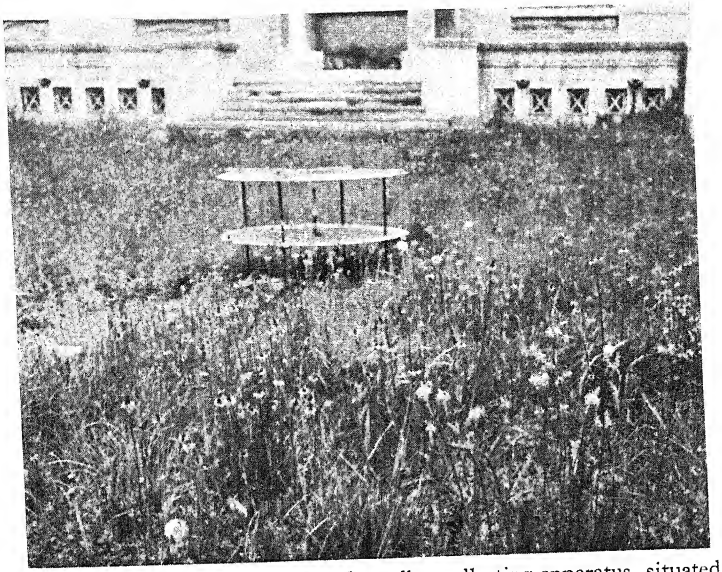
The weather conditions and the behaviour of the plants seem to have been more uniform during the four days 6, 7, 8 and 9 May than at any other time during the experiment, and it is therefore convenient to concentrate on the counts made for that period.

During that time the average gravity catch in 24 hr. was 1298 per 5 cm.^{2} and that by impact 5672 per 5 cm.^{2}, and the percentage ratio of deposition to impact therefore was $\frac{1298}{5672} \times 100 = 23\%$ (the corresponding figure for the whole fortnight was rather lower). Rempe (1937) showed that in various herbaceous plants, the average heights of whose flowers ranged between 0·2 and 0·55 m., the rate of pollen deposition on the ground varied between 150 and 33% of the impact catch at the height of the flowers, while in taller plants such as trees and shrubs it was much lower (e.g. in *Alnus*, 12·7 m., 2·3%). He concluded from these data, and from general considerations on the low degree of turbulence to be expected near earth level, that, in the air stratum lying between that level and say 50 cm., pollen deposition predominates over pollen drift: so much so, he argued, that it is a marked advantage in such plants if the male flowers are situated above the female flowers. Our data, owing to the fact that our gravity slide was placed 30 cm. above ground, are not quite comparable with Rempe's. Even so, our figure (quoted above) suggests a greater amount of drift from anthers at 40 cm. above ground than he will allow. This view seems to be borne out by a comparison between the rate of pollen liberation in the plantain-stand and that of deposition in our apparatus. Pollen output may be assumed to have remained at about the same level, throughout the four days referred to, as on the first of them (6 May) viz. $42{\cdot}4 \times 10^6$ grains per m.^{2}. Pollen deposition in our apparatus, however, averaged only $\frac{1300}{5} \times 10^4 = 2{\cdot}6 \times 10^6$ grains per m.^{2}. In other words, if we may assume our figures for deposition to be truly representative, of all the pollen liberated only about 1/16 failed to become air-borne.

It would be of interest, in view of the fact that the plantain-stand concerned must have been the chief source of such pollen in the neighbourhood, to relate the pollen production there to the pollen catch on the roof of the Museum, 100 ft. (=30 m.) away, viz. 12 grains per 5 cm.^{2} per diem on the average during the four days from 08.00 hr. on 6 May. The theory developed by Gregory (1945) on the decrease in density of spore clouds with increasing distance from place of liberation applies strictly however only to a point or line source; but the magnitude of the 'roof' catch would appear to be of the order to be expected.

(*b*) *Plantain pollen concentration in relation to allergy*

The experiments now described show that, in and near dense stands of *Plantago lanceolata*, the quantities of plantain pollen present in the air rise and fall very markedly with the time of day. In such neighbourhoods the consequent risk of inhaling large quantities of the pollen is greatest in the morning between 06.00 hr. and noon, after which it falls off rapidly and remains slight until the following morning. Once the season has begun, this periodicity is unlikely to be upset by anything but a drastic fall in temperature or continuous heavy rain in the early forenoon. We have previously shown (Hyde & Williams, 1944) that at Cardiff plantain pollen was on the average more abundant than grass pollen during May 1942; assuming, as we have good reason to believe, that this applies to Great Britain generally, it follows therefore that the main incidence of plantain pollen differs to some extent at least from that of grass pollen in time of year and time of day and in its response to external conditions, facts which should



Photograph A. General view of the site showing the pollen collecting apparatus, situated in the midst of vegetation dominated (temporarily) by *Plantago lanceolata*, and the Museum building in the background. Photographed on 6 May 1945 by A. E. Wade.

Photograph B. Typical plants of *Plantago lanceolata* forming part of the population concerned. Photographed on 6 May 1945 by A. E. Wade.

HYDE AND WILLIAMS—POLLEN PRODUCTION AND POLLEN INCIDENCE IN RIBWORT PLANTAIN (*PLANTAGO LANCEOLATA* L.)

be of assistance to allergists in determining to what extent, if at all, their patient's symptoms are to be attributed to plantain rather than to grass pollen.

VII. Summary

1. The atmospheric concentration of plantain pollen (*Plantago lanceolata*), as measured by the catch on adhesive slides exposed continuously and changed 2-hourly, has been studied at a site situated in the middle of vegetation dominated by the plant, and has been related to the time of flowering and to the weather conditions experienced.

2. On normally mild days the plant flowered profusely at or before 06.00 hr.; pollen liberation followed immediately after anthesis and local pollen concentration rose and fell correspondingly.

3. Flowering was markedly affected by temperature (when the temperature at the normal time of flowering fell below 45° F. it was delayed, and when the temperature remained below 50° it was almost entirely suppressed) but not at all by duration of bright sunshine recently experienced.

4. Data on pollen productivity are given and the proportion which becomes air-borne is discussed.

VIII. Acknowledgements

We desire to record our indebtedness to Dr D. G. Morgan for his constant encouragement, to the City of Cardiff Public Health Committee and Dr J. Greenwood Wilson for providing facilities at Llandough Hospital, and to the Council of the National Museum of Wales and Sir Cyril Fox (Director) for their continued support and for providing facilities for the exposing of slides at the Museum.

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FURTHER OBSERVATIONS ON *FRITSCHIELLA TUBEROSA* IYENGAR

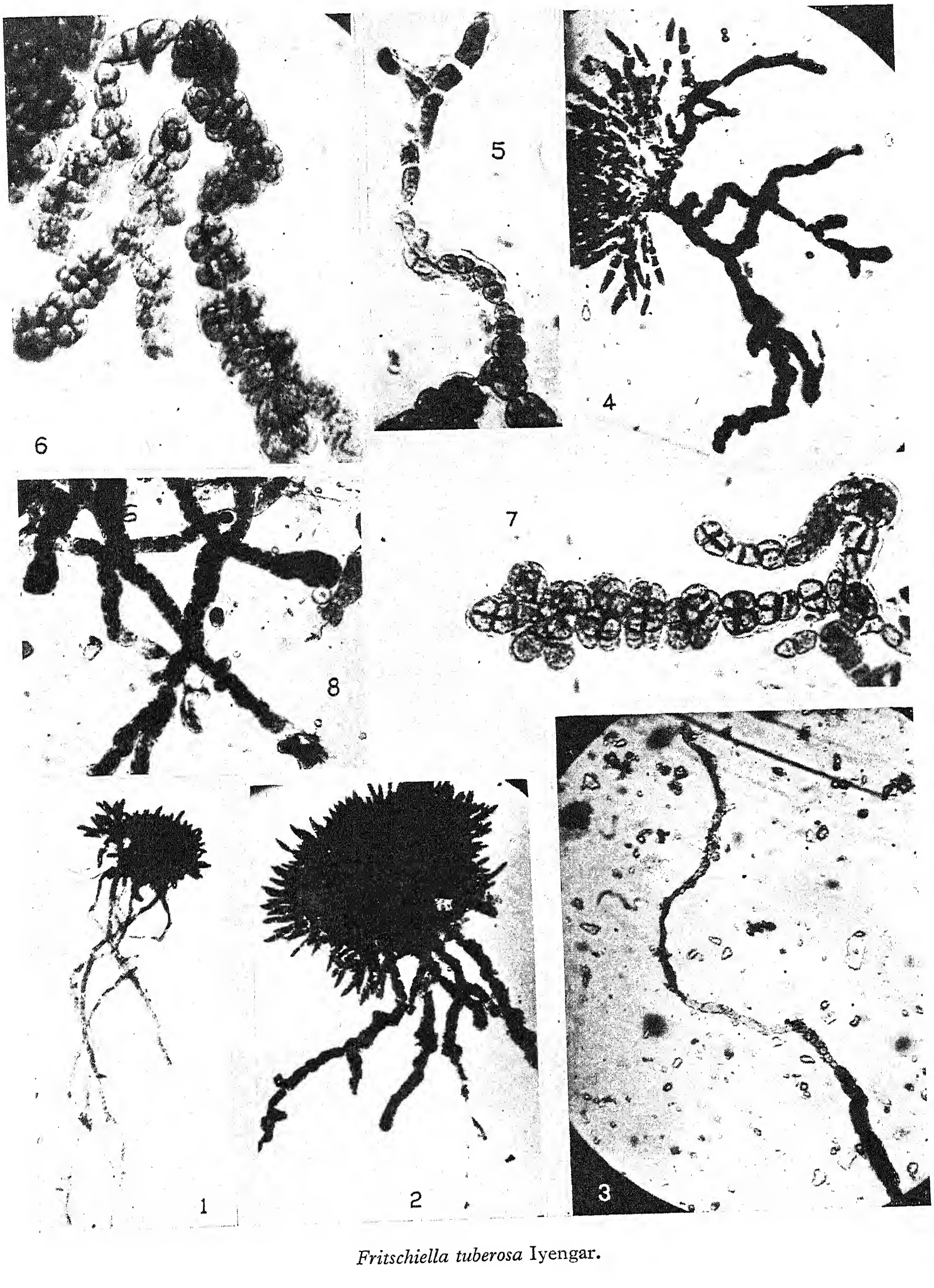
BY M. S. RANDHAWA

(With Plate 4)

Fritschiella tuberosa Iyengar was recorded by the present author from Fyzabad, U.P., India, in 1937. This alga again came under the present author's observation in January 1942, at Rae Bareli, a district in the Oudh province of the United Provinces, between the parallels 25° 49′ and 26° 36′ North latitude and 80° 41′ and 81° 34′ East longitude. There was an unusually heavy winter rainfall totalling 2·3 in. spread over a period of 5 days from 13 to 18 January 1942. Dark green specks of *F. tuberosa* about the size of a pin-head appeared on 20 January 1942, on a shady piece of waste-land. In about a week's time these specks spread into big patches entirely covering the soil. Ripe cysts were seen on 3 February. With the drying up of the soil, the green patches of *F. tuberosa* had become white in colour, and were distinguishable from crimson-red patches of *Protosiphon botryoides* Klebs. A few patches were ringed in green stages and kept under observation. By 10 February these patches had become white in colour due to the disappearance of chloroplasts from the sub-aerial part. They became rust-red by 12 February. These patches were watered with a hose for a week up to 18 February. From 19 to 21 February there was again a heavy rainfall, totalling 3·3 in., as a result of which the patches were inundated under water for about 4 days. Only very few specks showing young plants were seen. A latent rest period for the germination of cysts in this alga is indicated.

Usually *F. tuberosa* is found growing on manure heaps or in heavily manured fields with rich organic contents, particularly on areas fertilized with human excreta. Recently Ram Nagina Singh (1941) has recorded this alga from a 'tract of Parti or Usar land near Benares Hindu University'. 'Parti' means fallow land, and it is not unusual to see this alga growing on such land, but its record from alkaline 'Usar' land, impregnated with sodium carbonate and sodium bicarbonate is remarkable as well as unusual. So far as the present author's observations go, this alga grows only on heavily manured soil. A very rich growth of this alga was seen in a garden at Rae Bareli under a tree on which kites used to roost and the soil below was heavily manured with their droppings. It was also found growing on droppings of storks and geese along the banks of the river Jumna in green radial patches. It appears likely that it was collected by Singh from a patch of Usar fertilized by animal or human excreta.

Rhizoids. The present author had described the rhizoids of specimens collected from a pond at V. Chandipore in Fyzabad district as unseptate. Further observations on material collected from Rae Bareli have shown that rhizoids are septate with very thin hyaline septa. Excellent material showing well-developed rhizoids was collected from V. Mustafabad in Rae Bareli district on 5 February 1942. In some cases the rhizoids show extensive dichotomous branching with their tips slightly swollen (Pl. 4, fig. 1). The rhizoids are comparatively longer in younger plants in which the prostrate system is poorly developed, while in older plants they are not so prominent (Pl. 4, figs. 2 and 4).



Fritschiella tuberosa Iyengar.

Fig. 1. A young plant showing dichotomously divided rhizoids. Figs. 2 and 4. More mature plants with well-developed prostrate system. Fig. 3. A rhizoid. Figs. 5, 6, 7 and 8. Stages in the development of cysts.

RANDHAWA—FURTHER OBSERVATIONS ON *FRITSCHIELLA TUBEROSA* IYENGAR

Cyst formation. In 1939 the present author described early stages in cyst formation in this alga. Cysts are formed by thickening of the cell-walls of the cells of the subterranean prostrate system (Pl. 4, figs. 5, 6 and 7).

Singh (1941) has observed that swarmer formation is also confined to the cells of the prostrate system. As regards the possibility of occurrence of cysts, Singh had doubts. He observes: 'During the course of the study of the life history of the alga, the writer has not come across any cysts, but he has found a number of thick-walled zygotes and also rounded zoospores which have lost motility. They resemble to a very great extent the structures which Randhawa has described as cysts. His fig. 2(5) also appears to the writer to be a stage in the process of swarmer-formation, which has abruptly stopped due to sudden loss of water by intense evaporation from the soil.'

The present author did not find any empty cells in the prostrate system during his extensive observations on the living material, while, on the other hand, he found plenty of cysts, which are formed by direct conversion of the cells of the prostrate system into thick-walled rounded cysts. When the soil begins to dry up, the cells of the projecting system lose their chlorophyll and other cell-contents, though the cell-walls remain intact. The skeleton-like hyaline remains of the sub-aerial projecting system are usually found attached to clusters of light yellow cysts. At this stage the soil appears slightly whitish, on account of the disappearance of chlorophyll from the cells of the projecting system. Ripe cysts are orange-coloured, 12–24μ in diameter, and their tetrad-arrangement seen in early stages, persists for a long time (Pl. 4, fig. 6). In 1932 the present writer, along with Ghose (1933), described certain peculiarities in cyst-formation in *Protosiphon botryoides*. One of these was the occurrence of two to three irregular rows of cysts in the lower part. These multiserially arranged cysts are very probably those of *Fritschiella tuberosa* Iyengar, and do not belong to *Protosiphon botryoides*. Their multiseriate arrangement and the branched character of the containing filaments are indications that they belonged to *Fritschiella*. *Protosiphon* and *Fritschiella* usually occur intermixed and the only method of distinguishing them in a ripe state is to look for the above-mentioned characters.

According to the observations of the present writer, cyst formation is the common and prevalent mode of perennation in *Fritschiella*. Cyst formation, however, does not exclude the possibility of the occurrence of zygospores formed by the fusion of isogametes as described by Singh.

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THE IRISH SEA AS A PLANT BARRIER

By R. LLOYD PRAEGER

Dublin

Even assuming that the bulk of the present Irish flora arrived by means of land connexion with Britain in post-glacial or pre-glacial times (the evidence for the pre-glacial age of part of the flora appears to increase steadily), it cannot be doubted that many plants reached Ireland since separation was accomplished. Living all my life on the edge of the Irish Sea or the North Channel, I have watched continually for a sign of incipient colonization of this sort either by water or by air on the part of any native plant, but not even an enterprising alien has rewarded my vigilance; colonists of the latter class are all more or less obviously tarred with the brush of human influence. This is as might be expected, for the time factor heavily handicaps the chance of catching an immigrant red-handed; human life is too short, and human observation too discontinuous. One can point to certain Irish plants which are probably recent arrivals, in a relative sense—plants of very limited distribution there which one finds no reason to regard as relict—but one cannot do more than hazard a guess as to how or where they arrived, though they are believed to have come by natural means. Such are for instance *Geranium pratense* and *G. sylvaticum*, each occupying, in the whole of Ireland, only a limited area in Antrim, immediately facing Scotland; but the fact that they are plants with heavy seeds which fall rapidly in air and sink at once in water, renders difficult the idea of migration across even the narrow barrier of the North Channel. We have to call in birds to help us, and that I regard as savouring, in these cases, of intellectual bankruptcy.

The Irish flowering plants, indeed, seem to offer no direct evidence of actual present trans-marine migrational movement, though without doubt such migration is pursuing its slow natural course.

But if we turn to the ferns, I believe we can detect one or two instances of such movement from Britain to Ireland. The spores of ferns are so light, and are produced in such profusion, that the crossing of 50 or 100 miles of sea is of no account: it is the reception on the other side in a land already fully stocked, which may raise difficulties in colonization. Presumably because of its moist climate and greater proportion of unreclaimed or partially reclaimed land, Ireland has a fern population high in comparison with that of Britain—about thirty-three species in a conservative sense, against about forty. Some twenty-five of these thirty-three are widely spread, and no question arises in regard to them; but a few others have a very sparse and apparently fluctuating population, and their case deserves consideration. I may say at once, before going into details, that their behaviour in Ireland suggests that they are unsuccessful colonists there—up to the present at least—and that their continuance in Ireland is due rather to reinforcement from much larger colonies in Wales, northern England or Scotland, than to Irish parentage. Three species invite consideration:

Cryptogramme crispa. A total of about twenty or twenty-five plants has been found in Ireland as the result of a century and a half of botanical activity: they occur in the counties of Wicklow, Cavan, Louth, Fermanagh (an old unconfirmed record), Down, Antrim,

Derry and Donegal. They are mostly starved single plants; growing generally at from 1000 to 2000 ft.; most of the stations are in the north-east. Twice a plant has been found in Down and once in Wicklow in an artificial habitat—a pile of field stones or a loose wall—a few hundred feet above sea-level, and once equally low down among rocks under Fair Head in Antrim. A little plant found at small elevation on Bruse Hill in Cavan had a short life, being killed by drought in 1938, closely following its discovery. I have seen this fern in most of its north-eastern stations, and the contrast between these isolated starvelings and the luxuriant profusion of the plant in say Wales or the Lake District is startling.

Phegopteris dryopteris—reported from five counties—Clare, Wicklow, Sligo, Leitrim, Antrim—in each case, so far as known, as a single plant or clump, and never refound in any of its stations. All the records are now 50 to a 100 years old, but the Clare and Antrim records are backed by specimens, and the Leitrim station is well vouched for. The Clare station is described as 'roadside', and the Sligo station was on a roadside dry-built wall. The Leitrim and Antrim localities are on bare peaty hills, with few rocks and no trees. In view of the wide range of the oak-fern in Britain, and its usual profusion in the shaded places which it affects, its standing as a permanent member of the Irish flora is certainly open to suspicion.

Phegopteris robertiana—found a few years ago, for the first time in Ireland, forming a number of strong colonies in limestone crevices on a low hill near Headford, in Mayo—a quite characteristic habitat. There are hundreds of square miles of precisely similar ground not far away, especially in Clare, on which the abundant concomitants in its Mayo station, *Sesleria caerulea*, *Dryas octopetala*, *Geranium sanguineum*, *Gentiana verna*, etc., grow in profusion, but where the fern has never been seen. I take it that this may be certainly set down as a case of incipient colonization from some British colony, even though it occurs on the western side of Ireland.

One or two other cases may be mentioned of ferns not native to Ireland, and very seldom if ever cultivated in gardens there, as suggesting immigration from the east, though they are all found more sparingly in Britain than those dealt with above. Such are *Dryopteris rigida* (on a wall near Drogheda) and *Asplenium septentrionale* (on a wall in Down). Of one or two others one would like confirmation of name before discussing them.

Besides the Cranesbills referred to above, Ireland possesses a fair number of flowering plants confined to a single station, or to a couple of stations. Some of these are clearly glacial relicts, as they are in Wales and Scotland, others are survivors of the old coastal migration from the south (the Lusitanian element); but others again are very puzzling. Such as *Inula salicina* on Lough Derg in central Ireland (a widespread European plant absent from Britain), *Helianthemum nummularium* (one small patch on limestone in Donegal), *Serratula tinctoria* (a small colony by the river Barrow in the south-east), and others. These have a considerable range in Britain. Had the Neolithic climatic optimum been of any but short duration, one might be tempted to regard them as relict from that time, for the higher temperature which prevailed then undoubtedly was accompanied by migrations of both animals and plants. But that would involve a sea passage as long as at present, and of the three species mentioned *Serratula* alone is located near the eastern coast of Ireland. The more one studies the distribution of our plants and animals, the more difficult does it become, in most cases, to determine in any detail their past history from their present range. We must therefore hope that in the course of time fossil evidence will accumulate which will bring new light.

NOTE ON THE EFFECT OF TEMPERATURE AND OXYGEN ON THE VIABILITY OF COTTON SEEDS

By HUSEIN SAÏD

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It has long been established that dry seeds and spores can withstand extreme conditions of heat and cold without losing their vitality. This vitality is, however, lost very rapidly when the water content of these seeds and spores is increased. The writer examined the germination of cotton seeds (variety Ashmouni) after exposure to a temperature of 55–60° C. for fortnightly periods extending over 12 weeks. Aliquots of these seeds were surrounded by air, while others were put in a nitrogen atmosphere (devoid of oxygen) during exposure to the high temperature. The results of this investigation revealed that none of the seeds that were surrounded by nitrogen atmosphere and heated to 55–60° C. retained its viability. On the other hand, heating the seeds in the presence of air (oxygen) apparently did not cause any significant decrease in the percentage of germination except after the seeds had been exposed to the high temperature for 6 weeks or more. Seeds that were left in nitrogen at room temperature for 12 weeks, germinated quite successfully, the percentage germination being only slightly below that of the aerated control seeds (germination percentages being 66 and 72 % for the former and the latter seeds respectively). It seems, therefore, that neither heat nor anaerobiosis alone caused loss of vitality of the cotton seeds within the experimental period of 12 weeks, but when both were applied together, vitality was lost completely.

In this connexion mention must be made of the suggestion by Bělehrádek (1935) that the effect of high temperatures is similar to the effect of absence of oxygen in that, after a period of excitation, the vital activity is paralysed first temporarily and then permanently. According to this suggestion, high temperature and absence of oxygen would both be powerful agents in rapidly destroying the vitality of the seeds. Furthermore, Lantz (1927) reported that heating inactivates and destroys the enzymes in the seeds. Unpublished work by the writer also shows that enzymes may be inactivated in absence of atmospheric oxygen.

In the course of this work, the writer also examined the effect of freezing air-dried cotton seeds in solid CO_2 (temperature $-80°$ C.). Although the rate of germination was slowed down by freezing, yet the final percentage of germination was the same as that of the untreated seeds. The cotyledons of the frozen seeds always found difficulty in shedding the seed-coat, and even when the latter was shed, the cotyledons were mechanically injured and cracked.

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ADDRESS LIST OF BOTANISTS

IN COUNTRIES FORMERLY OCCUPIED BY THE ENEMY

SUPPLEMENT: December, 1946

The Editors of the *New Phytologist* publish this list to assist the re-establishment of communication with scientific colleagues. It is very incomplete and additions will be welcomed.

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BAUDYŠ, Doc. Dr Eduard. Alešova 27, Brno. (Phytopathology. Mycology.)
BAYER, Prof. Dr August. Murdered in the concentration camp of Mauthausen about 1942.
BĚLEHRÁDEK, Prof. Dr Jan. Albertov 4, Praha II. Rector of the Charles University. (Biology.)
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DYKYJ, Dr. Ústí nad Labem. (Biochemistry.)
FUTÁK, Dr Ján. Moskovská ul., Bratislava. (Geobotany of Slovakia.)
HADAČ, Dr Emil. Husova 5, Praha I. (Geobotany. Taxonomy of boreal flora.)
HERČÍK, Prof. Dr Ferdinand. Údohú, Brno. (Biology. Photobiology. Plant physiology.)
HORÁK, Dr Bohuslav. Kokycany, murdered in prison in 1942.
HRUBÝ, Prof. Dr Karel. Viničná 5, Praha II. (Cytology. Genetics.)
JEDLIČKA, Dr Josef. Kounicova 63, Brno. (Taxonomy. Bryology.)
JIRÁSEK, Dr Václav. Benátská 2, Praha II. (Taxonomy of Gramineae, useful plants.)
KAVINA, Prof. Dr Karel. Praha-Troja 207. (Applied Botany. Mycology.)
KLÁŠTERSKÝ, Dr Ivan. Zahradní 44, Praha XIX. (Taxonomy of Rosa. Taraxacum.)
KLEČKA, Dr Antonín. Výzkumné ústavy, Praha XIX. (Geobotany.)
KLIKA, Prof. Dr Jaromír. Píseckého 333, Praha XVI-Košíre. (Geobotany. Dendrology. Protection of Nature.)
KOŘÍNEK, Prof. Dr Jan. Viničná 5, Praha II. (Microbiology.)
KRAJINA, Dr Vladimír. Krocínova 3, Praha I. (Geobotany. Taxonomy of Hawaii.)
KRIST, Dr Vladimír. Brno, executed in concentration camp at Mauthausen.
MACKŮ, Prof. Dr Jan. Legionářská 14, Brno. (Mycology. Applied botany.)
MARTINEC, Dr Theodor. Kounicova 63, Brno. (Ecology.)
MIKYŠKA, Dr Rudolf. Náchod, Gymnasium. (Geobotany.)
MORÁVEK, Prof. Dr Vladimír. Kounicova 63, Brno. (Biochemistry.)
NÁBĚLEK, Prof. Dr František. Moskovská ul., Bratislava. (Taxonomy. Local flora.)
NÁBĚLEK, Prof. Dr Vojtěch. Bratislava, died 1940.
NĚMEC, Prof. Dr Bohumil. Na Václavce 1138, Praha XVI. Professor of Plant Physiology of the University in Bratislava. (Anatomy. Cytology. Physiology.)
NĚMEJC, Prof. Dr František. Václavské nám, Museum, Praha II. (Paleobotany.)
NOVÁK, Prof. Dr František. Benátská 2, Praha II. (Taxonomy. Local flora of Balkan Peninsula and Czechoslovakia. Pharmaceutical Botany.)
PASTYRIK, Dr L. Moskovská ul. 2, Bratislava. (Plant Physiology.)

interesting part of the book is Chapter IV, which deals with the mechanism of resistance and the effect of different factors on the outcome of the infection. In this chapter Prof. Gäumann has placed considerable emphasis on aspects which often receive scant attention in this country. His interests and contacts with medical pathology have clearly influenced him in this respect, and plant pathology should gain considerably. Most discussions of disease resistance in plants have been concerned with mechanical resistance in the form of thick cuticles or cork and gum barriers, or else in the variation brought about by different nutritional treatments. The examination of protoplasmic resistance has usually been cursory and unsatisfactory. This contrasts with medical pathology, where the study of disease resistance has centred primarily around protoplasmic resistance, antigens and the production of antibodies. From time to time individual workers have attempted to introduce similar ideas into plant pathology but seldom with much success. This may well have been due to the lack of a comprehensive statement of the problems along lines so familiar to medical workers. It is possible that in the present account Prof. Gäumann may have over-emphasized the similarities of reaction to invasion between plant and animal tissues. Even if this is so it will undoubtedly lead many plant pathologists to reconsider their results and see whether they might not be interpreted along these lines. The different types of symptoms, both morphological and physiological, which the host exhibits are summarized in Chapter V. The treatment of the physiological disturbances of the host is stimulating, and one hopes may serve to focus attention on an often neglected aspect of plant pathology. The book concludes with a brief account of the methods of combating disease.

It is inevitable that in a work which covers such a large field, certain aspects must necessarily be omitted. One omission which perhaps calls for comment is the absence of any discussion of the part played by pectic enzymes in soft rots. While admittedly our knowledge is small in this respect there have been numerous studies of fungal and bacterial pathogens which excrete extracellular pectic enzymes and attack the host tissue giving rise to typical soft rots.

The general appearance of the book is very pleasing and the choice of text-figures good. Unfortunately, some of the photographs have reproduced very poorly. There appear to be few printing errors, although several references to text-figures are incorrect, as on p. 43 where Abb. 280 should presumably be Abb. 177, and on p. 166 where Abb. 124 should be Abb. 123. The absence of any comparable book in the English language makes it extremely desirable that the work be translated into English as soon as possible, as most students of plant pathology will wish to refer to it frequently.

ALAN BURGES

Marine Microbiology. A Monograph on Hydrobacteriology. By Prof. CLAUDE E. ZOBELL. $6\frac{3}{4} \times 10\frac{1}{2}$ in. Pp. xv+240; 12 text-figures. Waltham, Mass.: Chronica Botanica Co. W. Dawson and Sons Ltd., London. 1946. \$5.

This book is a notable contribution to the literature of general microbiology. Dr Zobell has been actively engaged in research on problems of hydrobacteriology at the Scripps Institution of the University of California for the past fourteen years, and, with his colleagues, has published over forty papers in this field. Their work has always been characterized by a careful and critical approach to the special basic technical problems of marine bacteriology, notably those of sampling and counting, and the same careful evaluation of evidence is noteworthy throughout the present monograph.

As the subtitle suggests the book deals mainly with marine bacteria, although other micro-organisms are dealt with from the point of view of their interrelationships with the life of the bacteria, and a special chapter is devoted to aquatic yeasts and moulds.

It is estimated that 95 % of all bacteria in the sea are Gram-negative rods—a sharp contrast with soil where Gram-positive forms predominate. Facultatively anaerobic heterotrophic species are quantitatively the most important, and bacteria are far more numerous in the bottom deposits, even at great depths, than in the ocean itself. In general marine bacteria lead a life of austerity; most of the necessities, particularly organic nutrients, are in very short supply, and it is considered that the main factor controlling the size of the bacterial population is the very low concentration of organic material present. That which is available is utilized efficiently. The low temperatures (0–5° C.) at which the metabolic activities of marine microbes can still proceed is also striking. Much of great interest to bacterial physiology should come from the detailed study of marine types.

The first half of the book deals with the important technical problems of sampling and counting and with the general distribution and properties of the micro-organisms in the sea. There follows a section mainly devoted to the chemical transformations brought about by these organisms and the importance of these in the deposition of minerals and in the circulation of carbon, nitrogen, sulphur and phosphorus in the sea. The possible significance of marine bacteria in the formation of petroleum is also discussed. The book concludes with chapters on the microbiology of marine air and of inland waters and with a section on the more practical (sanitary and economic) aspects of marine microbiology.

There are over 600 references to original papers, but Dr Zobell succeeds in correlating the mass of experimental work and setting out the main issues with remarkable clarity. D. D. WOODS

An Introduction to the Taxonomy and Nomenclature of Fungi. By G. R. BISBY, M.A., Ph.D. $7\frac{1}{4}\times 5$ in. Pp. 117; two figures in the text. Kew, Surrey: Imperial Mycological Institute. 1945. Price 5*s*.

This short book has been written for those starting to study systematic mycology. The first part, comprising 40 pages, deals with methods of study. This part is extremely readable and will excite the interest of beginners and amateurs. It is hardly to be expected that it will kindle the initial spark of enthusiasm needed by the complete novice and, indeed, the early chapters are not written to that end, but plainly review the difficulties of the subject. It would be clear from the method of treatment, if one were not previously aware of it, that the author is writing from a wealth of personal experience, and that the advice proffered in this part of the book has sound practical backing. The chapter on measurement, however, would have been clearer if the object of measuring organs for description or diagnosis were made clear at the outset, and if the mean and limits of variation were both shown to be essential for these purposes. This subject, so important here as well as in other branches of biology, is treated in a manner less satisfactory than others.

The second part of the book—a further 65 pages—deals with problems of nomenclature and includes an account of the International Rules of Botanical Nomenclature, with exceedingly useful examples, notes and definitions. These are in the form of five introductory chapters followed by a copy of the rules with notes and examples.

Finally, there is a bibliography of fifty-six works covering aspects of all parts of the subject-matter of the book, followed by an index. The book will be helpful to young students, and the second part may constitute a readily available copy of the rules of nomenclature for others.

J. L. HARLEY

pH and Plants. An introduction for beginners. By JAMES SMALL, D.Sc. $8\frac{1}{2}\times 5\frac{1}{2}$ in. Pp. vii+216 with 16 figures. London: Baillière, Tindall and Cox. 1946. Price 12*s*. 6*d*.

One receives an initially unfavourable impression when confronted with several errors on the first page of this book. Mention of two will suffice; 'the concentration $[H_2O]$ = infinity' (this value is approximately 55·5, not infinity); 'the total of $[H^+ + OH^-]$ being constant' (the product, not the sum, is constant).

The unfavourable impression is strengthened as one reads on, finding phrases like '0·0000001 N-HCl = *p*H7 and is therefore neutral' which is an absurdity. 'The formula [for obtaining the buffer index] is... $\frac{\text{acid conc.}}{\text{per litre}}\times$ vol. used divided by shift in *p*H'; comment on the first term of this formula seems superfluous. Mistakes and ambiguities are too numerous to be quoted fully; those just mentioned above are a small random sample.

The book is said to be for beginners, yet no account is given of the dissociation of water beyond the 12-line paragraph which concludes with the statement that the sum (*sic*!) of hydrogen and hydroxyl ion concentrations is constant; dissociation of weak acids receives two lines, and bases, ampholytes and strong electrolytes are not dealt with. The second chapter is, however, devoted to buffers, but again there is no clear explanation of what buffering is; indeed the statement that HCl + NaCl is a buffer mixture (p. 12) increases the readers difficulty in interpreting such explanation as is given.

The greater part of the book, about 80 pages, is taken up with citation of such data as *p*H values of plant parts, *p*H optima of enzymes and isoelectric points of proteins. The interest of such data is strictly limited when there is almost no discussion of their significance or meaning. A change in *p*H of cell sap of a leaf, for example, as a concomitant of or causative agent of some physiological change is of some interest; but the metabolic reactions which control the *p*H values of plant tissues receive no mention by Prof. Small. *p*H values are presented as empirical data.

This applies also to the treatment of optima and of isoelectric points of proteins. *p*H optima of enzymes are cited, but no attempt is made to correlate them with isoelectric points or other properties of proteins. Numerical values for a number of protein isoelectric points are given, but the only explanation of the meaning or significance of the term isoelectric point is contained in the sentence 'the points on the *p*H scale where there is an equal balance between the acidic and basic properties of the proteins (and amino-acids) are known as isoelectric points'.

Some 50 pages are devoted to ecological relations. The empirical presentation may have some justification so far as some of the cited data are concerned.

This book stands condemned in the reviewer's opinion by the inadequacy, ambiguity and mistakes of the physico-chemical treatment, by similar qualities in parts of the physiological section of the book and by the failure to temper the empiricism of the physiological data with fundamental or theoretical treatment.

T. A. BENNET-CLARK

Laboratory Manual of Elementary Botany. By ARTHUR W. HAUPT, Ph.D. $9\frac{1}{4} \times 6$ in. Pp. 79; unillustrated. New York and London: McGraw Hill. 1946. Price 6*s*. 6*d*.

This Manual has, according to its preface, been revised to conform with the new edition of the author's *Introduction to Botany* for which it is the companion volume of practical instruction. This present edition consists of 116 short exercises, several of which may usually be completed in one practical period of two hours. A few take longer than two hours. The exercises are grouped under seventeen separate headings. The first ten deal with general elementary morphology, anatomy and physiology; the eleventh is a short group of two exercises upon Mendel's laws. Each of the last six groups deals with one of the larger sub-divisions of the plant kingdom and gives the elementary student an appreciation of the range of body construction and reproduction to be found within that sub-division. A sufficiently wide selection of forms is employed to avoid the worst faults of the 'type method' in elementary teaching.

In general arrangement, in order of presentation, in nature of the materials and in directions for working, the manual is very like others. It follows the almost universal and time-honoured mode of presentation of an introduction to practical botany. Perhaps it is too much to expect great originality in an elementary manual. Nevertheless, in the use of the heuristic method throughout, the course departs from the normal. The questions posed in each of the exercises can only be fully answered by careful observation and thoughtful interpretation. The whole course is, therefore, aimed to give a wide review of 'plant science' and a training in observation and reasoning.

Certain slips or errors cannot pass without remark. In Exercise 49 the use of two different drying methods '110° C. for a day or two' and '48 hr. at 95° C.' for control materials in the same experiment requires at least an explanation. Surely a reference to the radicle in describing the seed and germination in Exercises 64 to 67 should have been made. In this connexion the mode of describing the hypocotyl is misleading, if not definitely erroneous. In Exercise 60, the fourth line from the end should read 'three antipodal cells' not three synergids'. The use of simple reagents in making temporary mounts is not described except for a passing reference to the point that iodine will differentiate the nuclei. Surely a fuller description of the use of this reagent and also a reference to the value of aniline chloride might have been made.

The general directions which precede the exercises are sound and clearly written. Great stress is rightly laid upon the importance of full notes and careful drawings, but few would agree that finished Indian ink drawings are necessary or, indeed, an economic use of time, in an elementary practical course. The binding of the book is suitable to the hard wear of the laboratory and the print is clear and large enough to be followed when read upon the laboratory bench. The absence of illustrations is an advantage. In conclusion, the Manual will provide a satisfactory elementary course for those who cannot or do not wish to arrange one for their own type of student and their own local facilities.

J. L. HARLEY

American Species of Amelanchier. By G. N. Jones. Illinois Biological Monographs. Vol. XX, no. 2. 10×7 in. Pp. 126; 23 plates and 14 maps in the text. University of Illinois, Urbana, Illinois. 1946. $1.50.

This paper gives a complete systematic account of the American species of this well-known genus of Rosaceae (subfam. Pomoideae). There is a short introduction in which the author points out the difficulties in the taxonomy of the genus, which lie mainly in the variability of some of the species, particularly in the leaf-serration which has been much used in the classification in the past and in the difficulty of relating specimens at different stages of their growth. There is also a short paragraph on cytological work on the genus, but no details are given.

The greater part of the paper is, however, devoted to a taxonomic account of the eighteen species, two varieties and one hybrid, recognized by the author. The descriptions are good, and the practice of giving measurements of most of the organs of the plant may be especially commended. Other admirable features are the citation of localities and collectors in considerable detail and the provision of distribution maps for every species. It is to be regretted, however, that cross-references to the maps are not given, as they are sometimes separated by many pages from the species to which they refer. The type locality and whereabouts of the type specimen are given, as are short biological data on habitat and times of flowering and fruiting. Discussions on the relationships of each species and, where necessary, on the nomenclature, complete the individual accounts.

Separate keys are given to flowering and fruiting material, an example which might be more often followed in this country. They are eminently workable, and I have been able to identify, by their use, plants cultivated in this country.

The plates consist of photographs of the leaves of all the species and of herbarium specimens (often of the types) of many, and add considerably to the value of the work, as does the list of numbered exsiccatae.

No new species are cited as such by the author, but *Amelanchier neglecta* Eggleston, has, judging from the citation, not previously been published. No Latin diagnosis is given of this species, a defect which it is to be hoped the author will rectify. It may also be regretted that some account of the very few European and Asiatic species was not included for the benefit of workers on garden material.

A more serious regret may be expressed that the co-operation of a cytologist was not obtained. The chromosome counts of Sax and Moffett have shown that diploid and tetraploid forms both occur in the genus. It seems possible that a cytological investigation might provide a clue to the origin of some of the species of limited range which have been regarded as hybrids by some authors. These are reminiscent of the apomictic polyploid forms, of even more limited range, which occur in the allied genus *Sorbus* in Scandinavia and this country. Another point which would seem to merit experimental investigation is the possible existence of ecotypes in some of the more variable species, of which there is a suggestion in the account of *A. utahensis* and in the introduction.

The author is to be congratulated on an admirable account of a difficult genus, the variability of which is shown by the following quotation from the paper: 'there may now be found in botanical literature nearly two hundred binomials and trinomials representing the species of *Amelanchier* in America.'

E. F. WARBURG

Luther Burbank. A Victim of Hero Worship. By WALTER L. HOWARD, Ph.D., Emeritus Professor of Pomology, University of California. *Chronica Botanica*, Vol. IX, nos. 5/6, pp. 299–522, with 6 text-figs. and 7 plates. Waltham, Mass.: Chronica Botanica Co.; London: Wm. Dawson and Sons, Ltd. 1945–6. Price $3.75.

Towards the end of the last century, a young American, Luther Burbank, influenced by Darwin's *Cross- and Self-Fertilization in the Vegetable Kingdom*, set about the production of new varieties of fruits and flowers by crossing species and varieties on a huge scale and selecting desirable combinations in succeeding generations. He was extremely successful, and his 'new creations', as he called them, were often very great improvements. As his reputation grew, he came to be regarded by the American public as something of a magician; extravagant articles were written in his praise, while much pernicious nonsense was taught about him in American schools. He himself was not above exaggerating the value of his new plants, while firms handling them were only too ready to do

so. Too busy to write himself, he allowed 'editors' to write for him, and some of these indulged in the wildest extravagances and credited him with opinions and theories which he may never have considered before he received the manuscripts for approval. Such was his fame that he was posthumously honoured by portrayal on a postage stamp as one of America's greatest scientists, but he was denied his ambition of being recognized as a scientist by scientists.

Indeed, scientists as a whole were hostile to him, and when many of his claims were shown to be not well founded and some of his boosted varieties turned out to be failures, others hastened to attack him. The resulting controversy which raged in the U.S.A. had little repercussion over here, and probably most British geneticists who remember his name would dismiss him as a highly successful breeder of plants, whose results and ideas are of little value to genetical theory. This would perhaps be as well were it not that Burbank has been much quoted as an authority by Lysenko and his followers in the U.S.S.R. A reliable valuation of Burbank as a scientist would be useful to serious students of the 'new genetics'; and it is to be regretted that this essay by Prof. Howard will be of very little assistance to them.

Where we need an appraisal of the scientific value of Burbank's work and the validity and authenticity of scientific statements attributed to him by his editors, Prof. Howard has set out to show him as a victim of hero worship, and has done so in a wearisome series of character sketches which ramble disconnectedly with vagueness, repetition, and verbosity. We are told about Burbank the Man, the Nurseryman, the Scientist, the Egoist, the Mentor of Youth, the Unfortunate, the Pariah of Scientists, the Disappointed, the World Character, the Individualist, and about his Ethics, his Religion, his Foray into Science, his Admirers, his Detractors, and his Place in the Hall of Fame. But definite critical opinions are rarely given on important points, and in one instance where the author does commit himself, he makes a very poor case.

We are told, for example, that Burbank thought he was approaching the standing of a Messiah, and that 'he seemed to ignore all this experience with plants when he began to expound his theories about the betterment of people'. He did not keep proper records of his crosses, and his experiments were mostly uncontrolled; his aim was the production of better varieties, not the making of scientific discoveries. He preferred to explain his undoubted ability in selection in mystical terms. Yet, after a lengthy and wandering discussion of the question of whether Burbank really was a scientist, Prof. Howard arrives at an affirmative answer. He does so by the simple process of adopting a suitable definition for scientist.

Prof. Howard has clearly made a very extensive study of his subject, and the accuracy of the mass of historical facts which he presents is not to be doubted. But even if it were not unnecessarily long, this account of the Burbank background would be likely to be of little interest outside the U.S.A., and while it has a very important moral—the danger of extravagant exaggeration in the popularization of scientific discovery—the readers to whom this book is addressed are scientists who are only too well aware of the danger.

The book includes a 25-page summary, with descriptions, of the more important of Burbank's productions.

J. L. CROSBY

Trace Elements in Plants and Animals. By W. STILES. $5\frac{1}{4} \times 8\frac{1}{4}$ in. Pp. 189, with 12 plates. Cambridge University Press. 1946. Price 12*s*. 6*d*.

Research on the part played by trace elements in the metabolism of plants and animals dates back less than fifty years, except for certain isolated investigations. The momentum with which the work has proceeded, however, has been so great that it is extremely difficult to present a clear picture of the general position and to assess the value of much of the voluminous literature that has been written on the subject. Any attempt to do this, other than presenting a mere catalogue of papers, is inevitably weighted by the particular interests of the writer, and it is impossible for any one survey to cover all the aspects of the subject.

In the volume under review the historical introduction contains a useful list of plants for which the essential nature of certain elements is claimed, together with the investigator responsible. Warning is given that in some cases this claim is very tentative or even hardly justified, but the list provides a good starting point for future work. Approach to the subject is beset with difficulties owing to the minute quantities of the elements involved, and Prof. Stiles sets out various methods of purification of the materials used in culture experiments and the estimation of the quantities of micro- or trace elements present in plant materials. The use of the spectrograph has revolutionized

both the qualitative and quantitative sides of this question, and the description of the various methods of analysis used, both chemical and spectrographic, should provide a useful lead to workers in this field.

In describing the work on trace-element deficiency diseases in plants, attention has wisely been confined to four elements that are now almost universally acknowledged to be essential for many, if not all, plants—manganese, zinc, boron, copper—with the addition of molybdenum for which the evidence is more tentative. Although it has often been possible to prove that without these elements a plant cannot develop normally, there is still in many cases very little certainty as to the part played in the physiological functions by the minute traces that are necessary.

Manganese, zinc and copper appear to be associated with vital oxidations and reductions, but no one of these can replace another, and their functions can therefore not be identical. The manganese/iron ratio may be of importance, as pathological symptoms are developed if this ratio falls outside a certain range. Of the various theories of the part played by boron the most promising indicates a relation between boron and calcium, possibly with regard to the absorption and utilization of the calcium, but the results obtained with different species vary so much that no generalization is possible.

The work on trace elements in animals has so far made less progress. The effects of excess of selenium or molybdenum are well recognized, and evidence is accumulating of the importance of deficiency of copper, cobalt, manganese and iodine in relation to certain animal diseases. Comparatively little has yet been established as to the function of the trace elements in animals, although their presence in various organs has been proved.

The concluding remarks of this review point the way to future research, along pathological and physiological lines. Special attention may be drawn to the possible relationship of soil and climatic factors to the incidence of deficiency diseases, of which strong indications have been obtained with boron. A hint is also given of the possible importance of micro-organisms of the soil in this connexion, which is a field of investigation that has hardly been explored. Students, as well as research workers, will get an excellent bird's eye view of the subject from this volume, with helpful suggestions for obtaining further information on special points of interest. W. E. BRENCHLEY

An Introduction to Botany. By ARTHUR W. HAUPT. $8\frac{1}{4} \times 5\frac{1}{4}$ in. Pp. xii+425; 1 plate and 289 text-figs. New York and London: McGraw Hill. 2nd ed. 1946. 17*s*. 6*d*.

Prof. Haupt's book is a general introduction to botany at the Intermediate level. The first edition was reviewed in *The New Phytologist*, vol. 38 (1939). The reviewer then commended the morphological chapters and those on biology and heredity, but criticized the separation of the treatment of function and structure, and the level of the physiology. In his preface the author states that he has rearranged the matter so as to bring the study of the structure, gross and minute, and of the function of each plant organ together. The attempt to meet criticism is to be welcomed, but it has not been altogether successful. For, although the paragraphs dealing with function follow those dealing with structure in the chapter on each organ, there is still little interweaving of the treatment of the two. The physiology remains superficial.

But it must be agreed that the chapters giving a survey of plant life and those on biology are good. The material is sufficiently varied and abundant to maintain interest. The illustrations are excellent. The great majority are original and a considerable number of new figures have been added. The book concludes with a list of twenty-three botanical films, with the firms from which they can be obtained. M. SKENE

Crop Production and Environment. By R. O. WHYTE. $8\frac{1}{2} \times 5\frac{1}{4}$ in. Pp. 372; 32 plates and 53 text-figs. London: Faber and Faber. 1946. Price 25*s*.

This book is a review of recent research on plant development in relation to light and temperature, and deals mainly with vernalization and photoperiodism. It is arguable whether such reviews are best written by specialists who are themselves actively engaged in research in the field in question, or by professional abstractors whose business it is to read all the literature even remotely connected with the subject. Since, however, it is only rarely that an active investigator will spare the necessary time and energy from his researches to write a really comprehensive review covering a wide field, research workers should be grateful to Dr Whyte, who is in the second category, for bringing to

their notice a great deal of modern work on developmental plant physiology, much of it not easily available to the ordinary scientist, and in a format more attractive and palatable than the rather arid pages of abstracting journals. The author has had all the resources of the Imperial Agricultural Bureaux at his command and has made full use of them, gathering papers from publications both well-known and obscure. The book has both the merits and faults that would be expected where the author is not himself an investigator—there is an absence of that partiality with which the research worker usually discusses his own views and the searching criticism accorded to rival theories, but there is also a lack of any unifying viewpoint or co-ordination of the various subjects, such as is more likely to follow when the writer has a theoretical axe to grind, or at least has made a life-long habit of devising experiments to test a logical series of hypotheses.

The author in his preface likens himself to 'a reporter at a shadow conference at which plant scientists past and present have mingled with weather-wise farmers, gardeners with green fingers, and cultivators of all manner of crops in every cultivable latitude'. He states: 'I have attempted to bring out the views and experiences of all these people, in many cases using practically or actually their own words and jargon in order to report them accurately.' It is noticeable, however, that the practical men at the conference have very little to say, although Dr Whyte occasionally ventures a pious hope on their behalf, and the scientists, though they have a great deal to say, produce evidence of such complexity that the 'reporter', as he himself states in the Introduction, makes no attempt at 'sweeping generalizations'. The greatest use of the book, in fact, appears to be as a convenient introduction to the recent literature for the use of research workers on plant developmental problems. The author has adopted the expedient of quoting verbatim long passages or even almost complete articles from original publications, thus ensuring that no misinterpretation should creep into the presentation; it would have been preferable, however, to have denoted such verbatim paragraphs by inverted commas so that it might have been clear where the investigators were being reported in their own words. (Quotation marks are, however, inserted for certain passages of an obviously controversial nature.) The impression is frequently gained that Dr Whyte is presenting his own judgement where he is merely paraphrasing or quoting the original worker. The result is that he appears to be continually contradicting statements he has already made; with most confusing effect. In actual fact his own contributions are not conspicuous, most results and theories being presented without comment.

Although the book is to be welcomed as a useful aid to the research worker, who should consult the original publications and judge for himself of their merits, it may well be misleading for the student or the general reader. Indeed the title itself is misleading, for there is relatively little about crop production in the book. The presentation of such a mass of specialized research results without emphasis and almost without comment fails completely to give any perspective, nor will it be possible for the general reader to assess the soundness of the researches reported. In the case of such a rapidly advancing subject, which has attracted so vast a number of workers of such varying ability, some of the results must undoubtedly have been obtained by inferior experimentation, while the interpretations placed upon others may be unjustified by the evidence. For the student and general reader it is far more important that the reviewer should present a reasoned case than for the research worker, who may be expected to perform this task for himself.

At the outset the need to distinguish clearly between growth and development is stressed, but the suggested definitions share all the vagueness of Lysenko's original attempt. The difficulty appears to arise from the use of the word 'qualitative'. In certain cases postulated qualitative changes are equated with ascertainable morphological changes, but in the absence of such evidence the inferred qualitative changes are still held to occur with equal certainty. This lends to the discussions an abstract flavour which in no way elucidates the underlying mechanisms. The whole concept has been obscured by the uncritical adoption of the Russian theories of 'phasic development' in which indeterminate stages of development, unaccompanied by any external morphological signs, are postulated. One such stage, the so-called 'ripeness-to-flower' stage postulated by Klebs, has been identified by Purvis and Gregory during the elucidation of vernalization in cereals. It corresponds with the attainment of a certain minimum leaf number and thus acquires a definite status. This discovery is noted in a brief section at the end of Chapter II, but its insertion appears to have been an after-thought for later (p. 56) it is stated: 'The Russians assume that development towards reproduction begins as soon as the plant or germinating grain is exposed to the low temperature applied in vernalization. The "ripe-to-flower" condition recognized by Klebs is also development. In neither of these cases is the condition recognizable externally.' Again, on p. 76, Dr Whyte says:

'It has already been noted that the "ripe-to-flower" condition cannot be recognized by any morphological characters in the plant....'

Misprints, which do not affect the sense, are of importance only to the reviewer with nothing else to criticize, but those which completely alter the meaning are in another category. Two particularly bad examples are the following: p. 162, 'Foreseeing this objection, Gregory and Purvis pointed out that inhibition of all seeds in a sterilized solution was made at room temperatures...' (for 'inhibition' read 'imbibition'); p. 163, 'The auxin is detectable in the embryo either during development or during germination...' (for 'either...or' read 'neither...nor').

The book is nicely produced and the reproduction of the photographic illustrations is excellent. Unfortunately, the inadequate character of the descriptive legends reduces many of the illustrations to mere ornaments. It is generally necessary to turn up a page reference, often remote, for an explanation; in some cases this is so meagre and lacking in any interpretation of the significance of the effects shown as to be scarcely worth the trouble (e.g. especially Plate 9). The page reference for Plate 6 should be p. 79 and not p. 154 as stated. Some of the plates lack even a page reference and there is no simple way of finding out more about them than is provided by the brief caption: e.g. Plate 8, photo by Borthwick, Parker & Scully—there are no fewer than nine page references under Borthwick in the author index. Actually, the description of Plate 8 occurs in the text on a nearby page (p. 78), where it is given in error as Plate 5, but virtually no additional information is presented. A similar example of lack of a page reference is provided by Plate 12 (Photo. Withrow & Withrow—six page references in the author index) where the photoperiodic responses of three species to various wave-lengths are shown but the photoperiods concerned are not specified. Plate 20 (*b*) opposite p. 161 (Photo. F. G. Gregory), though a pleasant picture for its original purpose—an illustration for a popular article in the topical press—is without scientific value in the absence of any indication of species or treatment. A reference to this plate occurs on p. 249 but as there are thirty-five page references under Gregory in the author index there is little likelihood of any reader persevering in tracking it down.

It may appear that the matters of misprints and descriptions of the plates have been unduly laboured, but they detract seriously from the only justification for a book of this kind, namely that it provides a useful addition to the working library of the research worker in the field considered. In spite of them it is still to be recommended for that purpose, for the work it describes is not to be found collected together elsewhere.

O. V. S. HEATH

Principles of Agricultural Botany. By ALEXANDER NELSON. $8\frac{1}{2} \times 5\frac{1}{2}$ in. Pp. 556, with 17 colour plates, 128 half-tone and 182 text illustrations. London: T. Nelson and Sons, Ltd. 1946. Price 35*s*.

There are but few British text-books dealing with applied botany; the publication of a new one is, therefore, a matter of keen interest to student and teacher.

In his preface the author considers that the knowledge most useful to agricultural students who may expect to see farming under a wide diversity of natural conditions, is a knowledge of principles; he has selected his material to meet this requirement. His aim is thus to arouse interest rather than only to provide material likely to satisfy some examiners.

Opening with some slight hesitation, the first few pages concern the nature and composition of common substances found in plant tissues, and serve as an introduction to the section dealing with elementary morphology and anatomy which follows along conventional, but well established, lines: except that the text is ably illustrated by a fine series of photo-micrographs, of which a few are in colour. There is a brief review of certain methods of vegetative propagation followed by a more detailed study of the floral structure, especially of the cultivated grasses.

The second section concerns physiology, and introduces the reader to the concept of permeability, to the process of osmosis, to the water relationships of the plant both from the more physiological and ecological aspects. Recent American work on the selective accumulation of inorganic nutrients and recent British investigations of mineral deficiencies are discussed; but when dealing with other topics, with respiration, with fermentation, for example, the discussion of modern work is limited, nor are the practical applications such as the gas storage of fruits or the malting qualities of barley pointed out. The author shows a wise discretion in his review of such controversial matters as vernalization and phasic development. The chapter on seed germination is well written and the illustrative data are well selected.

Perhaps a section headed 'Agronomy or Applied Ecology' would have been convenient and advantageous; the chapter on pastures might have fallen there, to be accompanied by a similar one dealing with cereal crops. From his widely-gained experience the author brings together results gained at the Waite Agricultural Institute and places them alongside those obtained at the Welsh Plant Breeding Station for comparative study of pastures.

The third section deals with weeds and diseases, and mentions pests. Virus diseases are lightly touched upon and only thirty pages can be spared for the mycological aspect of pathology. Thus, the student is not here given a thorough introduction to the nature and life of a parasitic fungus—that remains for the practical class—yet such has been proved a necessity in the teaching of agricultural and horticultural students. The section forms an admirable, but cursory, general introduction to the commoner diseases.

The final section concerns plant breeding and introduces the reader to Mendelism, to polyploidy and to hybrid vigour, but the text does not trace out the production of the Yeoman wheats or similar examples of genetical achievement.

Throughout, the text generally reads easily and the meaning is clear. The author very frequently makes figurative use of words in contexts to which they are not literally applicable, this is usually effective and in all cases the occasion is marked so that confusion should not arise—he warns his readers against the dangers of adopting such terminology as analogies may prove false (p. 359).

The publishers have spared little expense in the production of this book with its bold type, adequate spacing, profuse illustrations, tabular presentation of certain data, lists of books for further reading, and useful index. All these features should make this a book likely to prove attractive to students and will help the author to attain his end in arousing their lasting interest in the principles underlying the study of cultivated plants. M. A. H. TINCKER